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A History of Sockeye Salmon Research, Karluk River System, Alaska, 1880–2010

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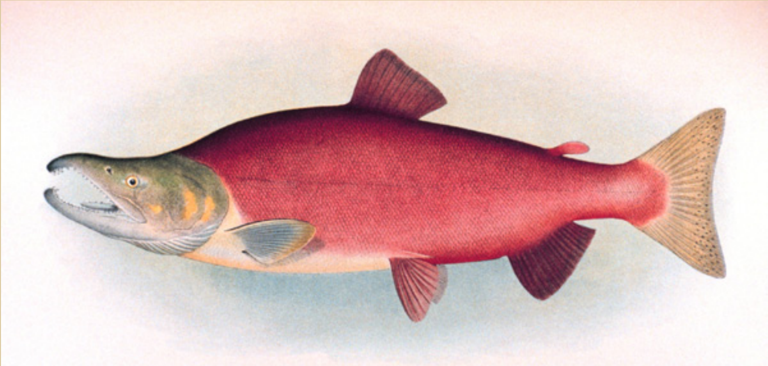
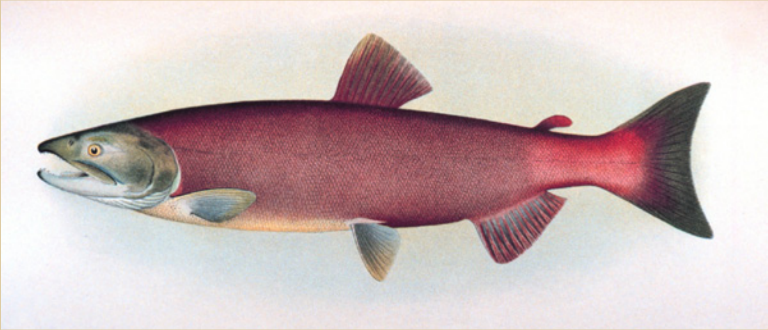



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Richard Gard and Richard Lee Bottorff

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Author contact information:

Richard Gard
2670 Fritz Cove Road
Juneau, AK 99801

Richard Lee Bottorff
1963 Toppewetah Street
South Lake Tahoe, CA 96150
email: richbot@yahoo.com

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Dedication

We dedicate this book to Georg Wilhelm Steller (1709–1746), Alaska's first scientist. Steller first described the anadromous life cycle of North Pacific salmon and identified sockeye salmon by its present scientific name *nerka*, a term originally used by the Koryak people of Kamchatka (Steller, 2003).

Contents

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Special appreciation is given to the many field biologists and fisheries historians who loaned us historic photographs of Karluk: Joseph Thomas Barnaby, Catherine DeLacy (for Allan C. DeLacy), Benson Drucker, Jean R. Dunn, Jim Finn, Arthur Freeman, Lynn Gabriel (for Tom Barnaby), John Q. Hines, Mark R. Jennings, Jerry R. Loll, Robert S. Morton (for Mark Morton), Philip R. Nelson, Jerrold M. Olson, John B. Owen, Robert F. Raleigh, Timothy L. Smith, Clark S. Thompson, and Charles E. Walker. We thank Karen Hofstad (Petersburg, AK), Warren E. "Nick" Nickell (Seattle, WA), Terry Kovel (Beachwood, OH), Richard C. Sturgill (Blaine, WA), Lantern Press (Seattle, WA), Alaska State Museum (Juneau), and Pratt Museum (Homer, AK) for the Karluk salmon canning labels. This book benefited from the historic photographs and collection resources at the Anchorage Museum at Rasmuson Center, Alaska Packers Association Museum, Alaska State Archives, Alaska State Library Historical Collections, Alaska State Museum, Baranov Museum, California Academy of Sciences Archives, Fisheries Research Institute Archives, NOAA Auke Bay Laboratory, NOAA Internet Photo Library, Maine Maritime Museum, Pratt Museum, San Francisco Maritime National Historical Park Museum Collections, Smithsonian Institution, U.S. Coast Guard Historian's Office, U.S. Fish and Wildlife Service National Digital Library, U.S. National Archives Anchorage, and University of Washington Special Collections Division. We greatly appreciate the courtesies given by all individuals and institutions for the many historical images used in this book.

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Acronyms

ABL	Auke Bay Laboratory
ADF	Alaska Department of Fisheries
ADFG	Alaska Department of Fish and Game
APA	Alaska Packers Association
ARLIS	Alaska Resources Library and Information Services
ASA	Alaska State Archives
BCF	Bureau of Commercial Fisheries
BSFW	Bureau of Sport Fisheries and Wildlife
FRED	Fisheries Rehabilitation, Enhancement and Development Division, ADFG
FRI	Fisheries Research Institute, University of Washington
FWS	Fish and Wildlife Service (1940–1955)
NARA	National Archives and Records Administration
NMFS	National Marine Fisheries Service
NOAA	National Oceanic and Atmospheric Administration
RG	Record Group
UAF	University of Alaska, Fairbanks
USBF	U.S. Bureau of Fisheries
USFWS	U.S. Fish and Wildlife Service (1956–present)

CHAPTER 1

Introduction

Karluk River sockeye salmon—a wonder of the natural world.

One of Alaska's most famous runs of sockeye salmon, *Oncorhynchus nerka,* returns each year to spawn in the pristine waters of the Karluk River drainage on Kodiak Island. The sheer magnitude and long duration of the run are remarkable. Within recorded history, this run has, in peak years, exceeded 4,000,000 fish, a wondrous spectacle of nature. This abundance is particularly striking since, physically, the Karluk River is relatively small when compared with other notable salmon-stream systems of Alaska and the Pacific Coast. Such vibrant profusion has riveted human attention for as long as people have occupied Kodiak Island, an interest most often centered on the high value of these salmon as human food, for both direct subsistence and commercial profit. This species also has been intensely scrutinized by scientists for well over a century, with the goal of understanding all features of its life history and biology that help to sustain healthy runs. Likewise, attention has been focused on these sockeye salmon for aesthetic and spiritual reasons, to appreciate the untold intricacies and innate diversity of life that so superbly thrives in the beautiful Karluk River ecosystem.

Kodiak Island, often labeled as Alaska's "Emerald Isle" for the bright verdant plant life that flows across its mountains each summer, is located in the Gulf of Alaska about 50 km southeast of the Alaska mainland and across Shelikof Strait (Fig. 1-1). Being the largest island of the Kodiak Archipelago, it is positioned near the active junction of the Pacific and North American tectonic plates, a geologic location with considerable consequences (earthquakes, tsunamis, and volcanic ash falls) for humans and other life. Formed and buffeted by massive tectonic and glacial forces, Kodiak Island has experienced several cycles of complete elimination and reinvasion of its flora and fauna over the past 1,500,000 years as immense glaciers advanced and retreated across the landscape (Karlstrom et al., 1969).

During the last cycle, glaciers that had covered most of the island withdrew some 10,000 years ago, and life once again spread across the terrain and into its lakes and rivers. On southwest Kodiak Island, eleven fish species invaded Karluk Lake and River, seven of these being salmon, steelhead, and Dolly Varden that spend part of their life cycle in freshwater and part in the ocean (Table 1-1). The Karluk ecosystem, with suitable spawning sites and a large nursery lake, was ideal for sockeye salmon to flourish and, as a result, several million adult fish returned to spawn each year. This apparent limitless bounty of sockeye salmon was a central reason for Karluk's widespread fame.

Humans first arrived on Kodiak Island over 7,000 years ago and have resided along the Karluk River for at least the past 5,000 years. Archaeological surveys document the many sites of human habitation that existed along the river and lake. Besides the permanent residents, additional people moved to Karluk each summer from nearby winter camps to access its rich salmon resources (Knecht and Jordan, 1985; Knecht, 1995). In particular, the indigenous Alutiiq people and their ancestors have maintained a village for millennia near the

Table 1-1
Fishes of Karluk Lake and River, Kodiak Island, Alaska.

Scientific name	Common name	Level of abundance	Life cycle
1. *Cottus aleuticus*	Coastrange sculpin	Common	R[1]
2. *Gasterosteus aculeatus*	Threespine stickleback	Abundant	R
3. *Pungitius pungitius*	Ninespine stickleback	Few	R
4. *Oncorhynchus gorbuscha*	Pink salmon	Abundant	A[2]
5. *Oncorhynchus keta*	Chum salmon	Few	A
6. *Oncorhynchus kisutch*	Coho salmon	Common	A
7. *Oncorhynchus mykiss*	Steelhead/Rainbow trout	Common	A/R
8. *Oncorhynchus nerka*	Sockeye salmon	Abundant	A
9. *Oncorhynchus tshawytscha*	Chinook salmon	Common	A
10. *Salvelinus alpinus*	Arctic charr	Common	R
11. *Salvelinus malma*	Dolly Varden	Abundant	A/R

[1]R = Resident in freshwater.
[2]A = Anadromous.

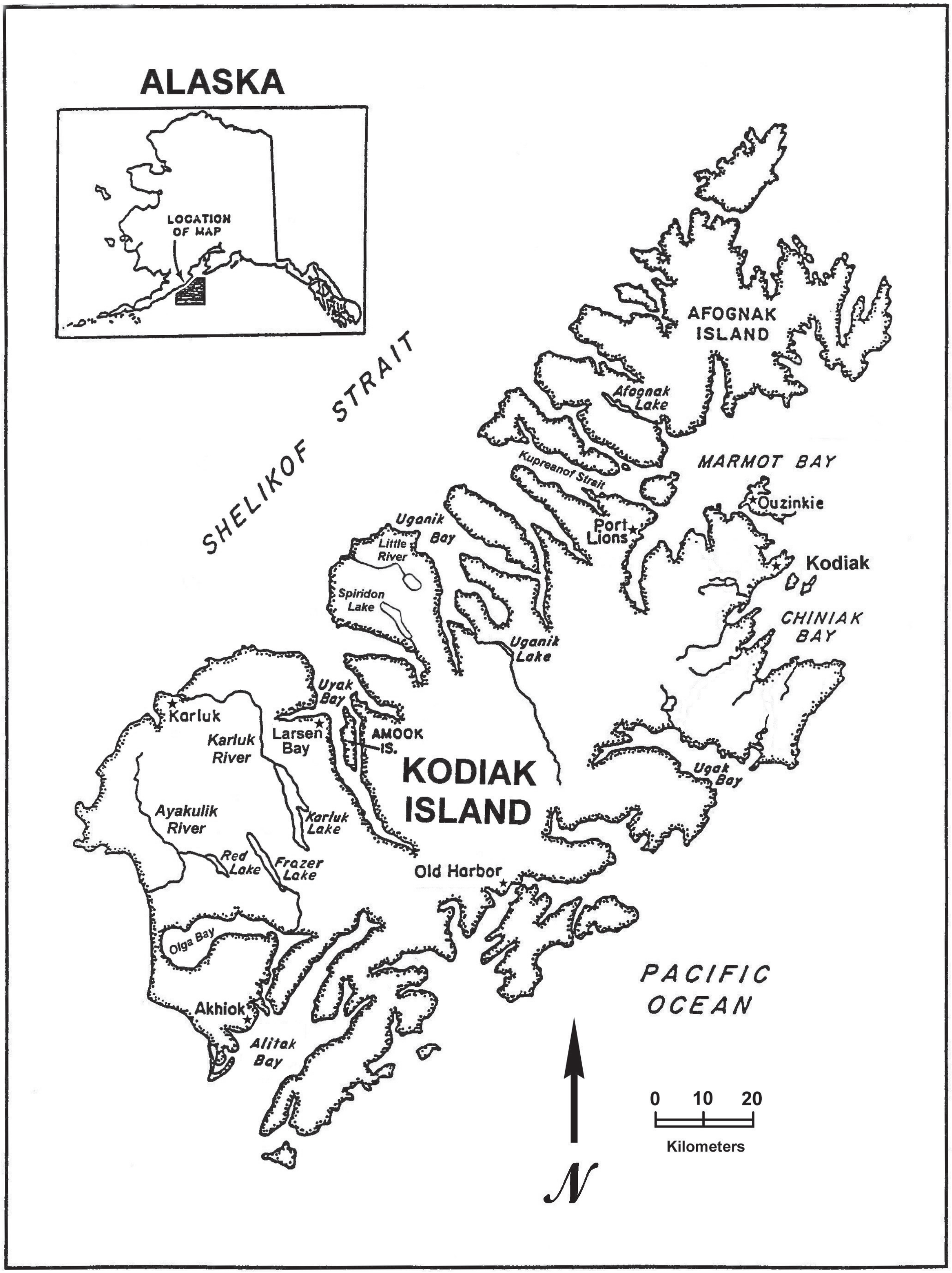


Figure 1-1. Map of Kodiak Island. (Modified from Barrett and Nelson, 1995.)

river's mouth, a strategic location for garnering food from the river, intertidal zone, and open ocean.

Although the early Karluk inhabitants heavily relied on the nearby marine resources in Shelikof Strait, they also settled beside the river and lake because abundant runs of sockeye salmon provided them with a dependable, nutrient-rich, food source. Fittingly, the name "Karluk" is derived from the Alutiiq word "iqalluk," a term used for fish. Fresh salmon could be caught in the river for at least half of the year, and by drying and storing these fish, sufficient provisions could be easily secured for later use in winter and early spring when adult salmon were absent. It appears that these early subsistence harvests of sockeye salmon were easily supplied by the profuse annual runs, even though early human populations in the Karluk vicinity may have approached 1,000 (Lisiansky, 1814). And yet, human reliance on Karluk's salmon undoubtedly varied over the millennia as long-term climatic changes affected the productive capacity of marine and freshwater food sources (Knecht, 1995; Finney et al., 2002).

During the period when Russia controlled Kodiak Island (1784–1867) and Alaska's fur trade in sea otters, *Enhydra lutris*, sockeye salmon from the Karluk River were regularly harvested, dried or salted, and distributed to sea otter hunters and support personnel at Karluk and other locations along Alaska's coast. The fur traders and officials of the Russian-American Company clearly recognized the value of these salmon resources and used Karluk as a vital provisioning base for their overall commercial ventures in Alaska for more than 80 years. Because these food supplies supported a much larger population than just the local residents of Karluk Village, sockeye salmon harvests may have been somewhat larger during the Russian era. Reportedly, several hundred thousand salmon were dried each year at Karluk in the early 1800s. These fish were easily procured by placing wood and rock barricades (known by the Russian term "zapors") in the river to block and concentrate the upstream migration (Pierce, 1978; Tikhmenev, 1978).

The first U.S. salmon cannery in southwestern Alaska was built on Karluk Spit at the mouth of the Karluk River in 1882, and it operated without competition for the next five years. The river's enormous runs of sockeye salmon, still strong despite the previous era of Russian harvests, easily supplied the entire cannery demand of 58,800 fish in 1882. But harvests continued to increase each year and reached 1,004,500 fish in 1887. The cannery's case pack production was shipped south 3,200 kilometers (2,000 miles) each year to San Francisco for sale and distribution.

Following the commercial success of this single cannery during 1882–87, five additional canneries were built on or near Karluk Spit in the next few years, and at least five other canneries that took salmon from the Karluk River were built at further locations around Kodiak and Afognak Island (see salmon canning labels in Photo Supplement that begins on page 19). Consequently, under intense competition between the canneries, annual harvests of Karluk River sockeye salmon quickly reached several million. In fact, their total case pack during the early years of the fishery made up a major proportion of that produced from all of Alaska. In 1893, most of Karluk's canneries were consolidated into the newly incorporated Alaska Packers Association (APA), with headquarters in San Francisco. The APA became the dominant cannery at Karluk for many decades.

Karluk Spit salmon canneries and Karluk River (right), 1897. (Frederic M. Chamberlain or Harry C. Fassett, from Moser, 1899)

Beach seining for sockeye salmon at Karluk Spit, June 1906. (John N. Cobb, University of Washington Libraries, Special Collections, Cobb 2390)

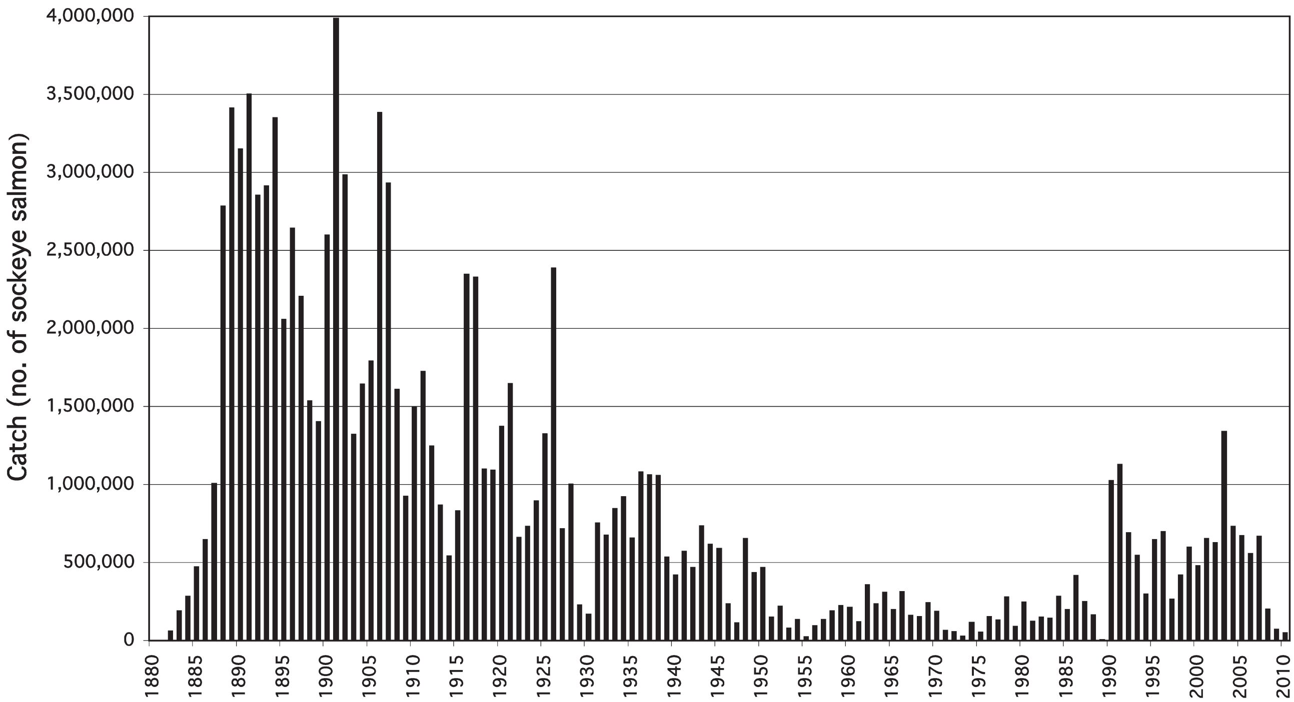


Figure 1-2. Karluk River sockeye salmon catch, 1882–2010. Sources: 1) 1882–1984: Ken Manthey, Dave Prokopowich, and JoAnn Strickert. 1984. 1984 annual finfish management report, Kodiak Management Area. ADFG, Division of Commercial Fisheries, Kodiak. Unpubl. rep., 338 p.; 2) 1985–2010: ADFG data files, Division of Commercial Fisheries, Kodiak.

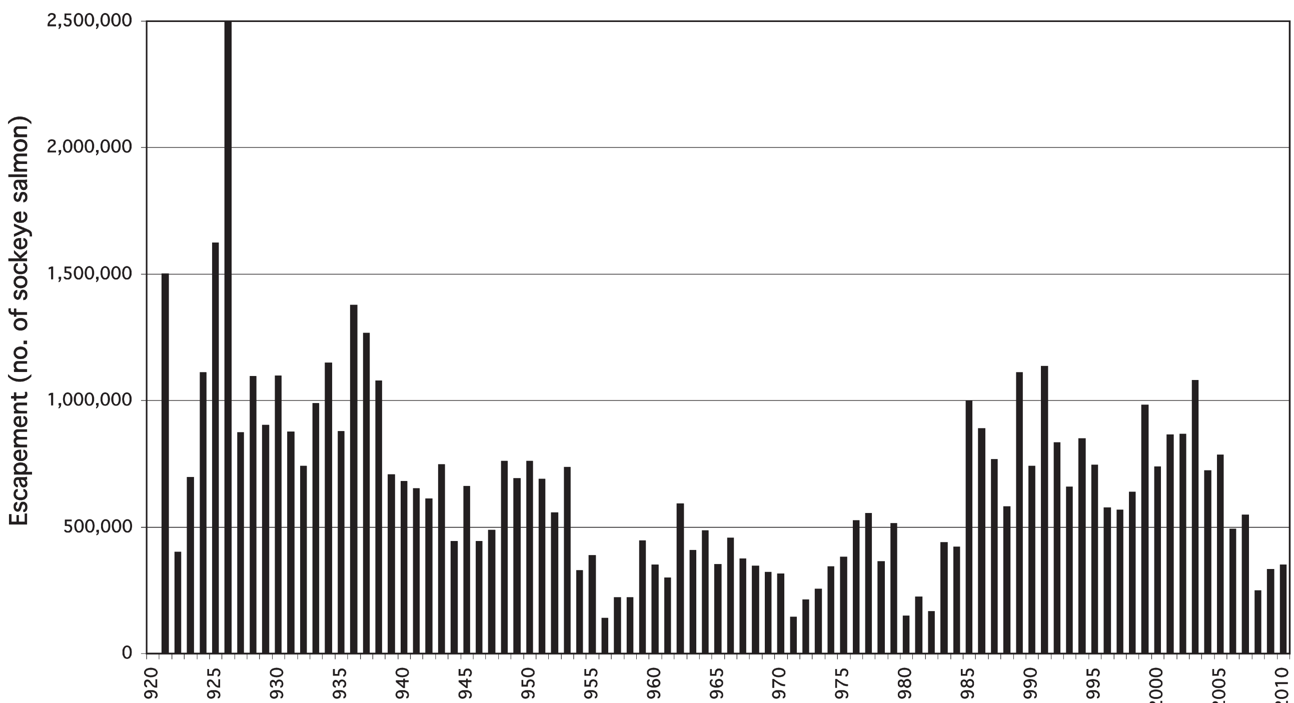


Figure 1-3. Karluk River sockeye salmon escapement, 1921–2010. Sources: 1) 1921–1984: Ken Manthey, Dave Prokopowich, and JoAnn Strickert. 1984. 1984 annual finfish management report, Kodiak Management Area. ADFG, Division of Commercial Fisheries, Kodiak. Unpubl. rep., 338 p; 2) 1985–1988: Malloy and Prokopowich (1992); 3) 1989–1996: Brodie (1996); 4) 1997–1998: Kuriscak (2004); 5) 1999–2008: Caldentey (2009a); 6) 2009–2010: Tiernan (2011).

As a result of these commercial enterprises, Karluk's bountiful sockeye salmon runs soon became widely known to many cannery personnel, fishermen, fishery inspectors, governmental officials, fishery biologists, visitors, and residents of Alaska and the Pacific Coast. Typically, written accounts of Karluk prior to 1900 marveled at its outstanding salmon runs. For example, Marshall McDonald, U.S. Commissioner of Fish and Fisheries, boasted in 1894 that "the Karluk River, on Kadiak Island, is probably the most wonderful salmon river in the world."

Despite the glowing reports about Karluk's salmon resources, the peak cannery production of 1888–94 was followed by 90 years of declining harvests and increasing debates over the cause of this reduction (Figs. 1-2 and 1-3). Governmental officials and fishery biologists sought to reverse this negative trend by imposing various regulations on the fishery and striving to understand the biological factors that controlled sockeye salmon abundance. Accordingly, a long-term program of biological research on sockeye salmon began in 1921 with the installation of a weir on the Karluk River to count the number of fish that reached the spawning grounds at Karluk Lake and to gather basic data on their age, length, weight, and sex.

As these fishery statistics were collected and analyzed, biologists began to advance different theories to explain what had caused the decline in the runs. Over the years, the number of theories grew and many prominent biologists became involved in this scientific controversy. The progression of the debate was followed not only by those directly involved in defending a particular theory, but also by the worldwide fisheries community that knew about Karluk's previous prolific runs, their subsequent decline, and the ongoing research. Thus, for most of the 1900s, the sockeye salmon runs at Karluk also were famous because of their long-term decline, attempts to explain the decline, and the biological research devoted to understanding this species.

While there has never been a formal end to the debate over the causes of the long-term decline, continuing research led many of the proposed theories to be set aside as implausible. Overfishing was most often viewed as the culprit at Karluk, but discussions continued about just how the commercial harvests had affected different biological mechanisms and led to progressively fewer returning salmon.

When Karluk's sockeye abundance greatly rebounded beginning in the mid 1980s, with runs often exceeding 1,500,000 fish, the emphasis of fisheries research shifted away from trying to explain the long-term decline, to understanding and perpetuating the growing success. Yet, with the intrinsic complexity of the interacting physical and biological factors at Karluk, it was not always obvious how much of any observed change in salmon abundance came from human management and how much came from uncontrolled, and partially unknown, environmental factors. That is, was human management solely responsible for reversing the long-term decline or did a particularly beneficial set of natural environmental conditions increase the salmon runs?

After two decades of highly successful sockeye salmon runs at Karluk (1985–2007), management of this fishery is on a solid scientific foundation, though it is also known that salmon populations respond to large-scale, long-term, environmental conditions in the North Pacific Ocean that are largely beyond human control (Finney et al., 2002; Clark et al., 2006; Martinson et al., 2008, 2009a, b). Thus, many important topics remain to be studied for sockeye salmon. Fortunately, individuals and institutions still have an intense desire to better understand this salmon species and continue to pursue the worthy goal of ensuring abundant and sustainable runs to the Karluk River.

Karluk Lake and River

Karluk Lake, located on southwestern Kodiak Island and the largest lake on the island (lat. 57°22′ N; long. 154°02′ W; Fig. 1-4), was formed many thousands of years ago by glacial scour and moraine deposits in a northwest trending valley flanked by rugged mountains that rise to elevations of 750–900 m. Having three internal lake basins and a surface elevation of 112 m, Karluk Lake is 19.6 km in length and 3.1 km in width at its maximum. Lake waters are clear, cold, and oligotrophic; summer surface temperatures seldom exceed 15°C and ice covers the lake in winter. The region has a maritime climate, with mild temperatures, moderate precipitation of 172 cm per year, and frequent cloudy skies. The lake and surrounding landscape are pristine wilderness. Terrestrial vegetation, still in a long-term succession after the last glaciers receded, is a luxuriant covering of grasses, sedges, herbs, shrubs (alder, willow, birch, elderberry), and cottonwood trees. Unlike northeastern Kodiak Island, conifer forests are absent in the Karluk area.

More than 15 small creeks and two larger rivers flow into Karluk Lake (Fig. 1-5). The small creeks, important spawning habitats for sockeye salmon, descend steep mountain slopes and often have waterfalls and

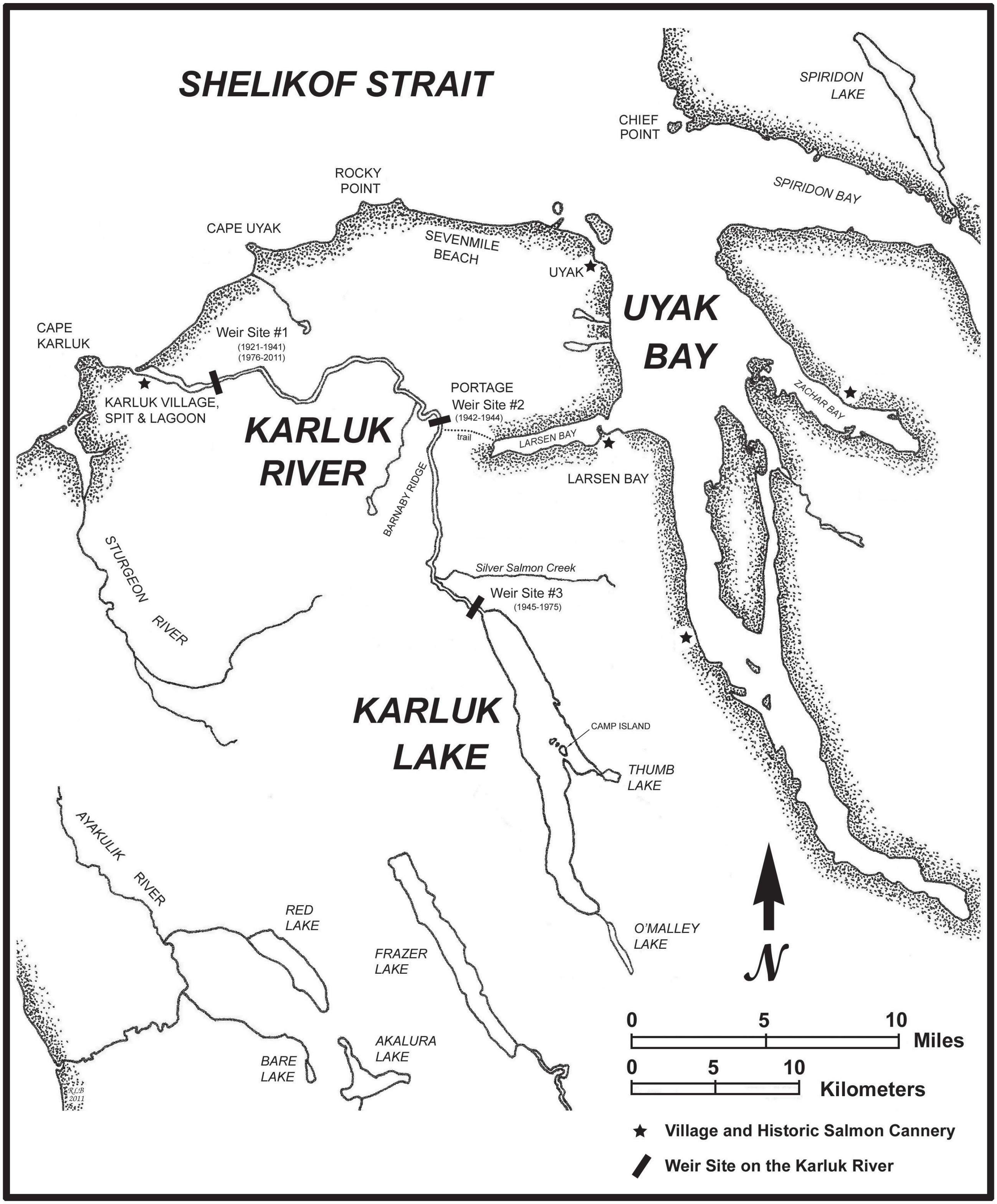


Figure 1-4. Map of the Karluk River watershed and southwest Kodiak Island, Alaska.

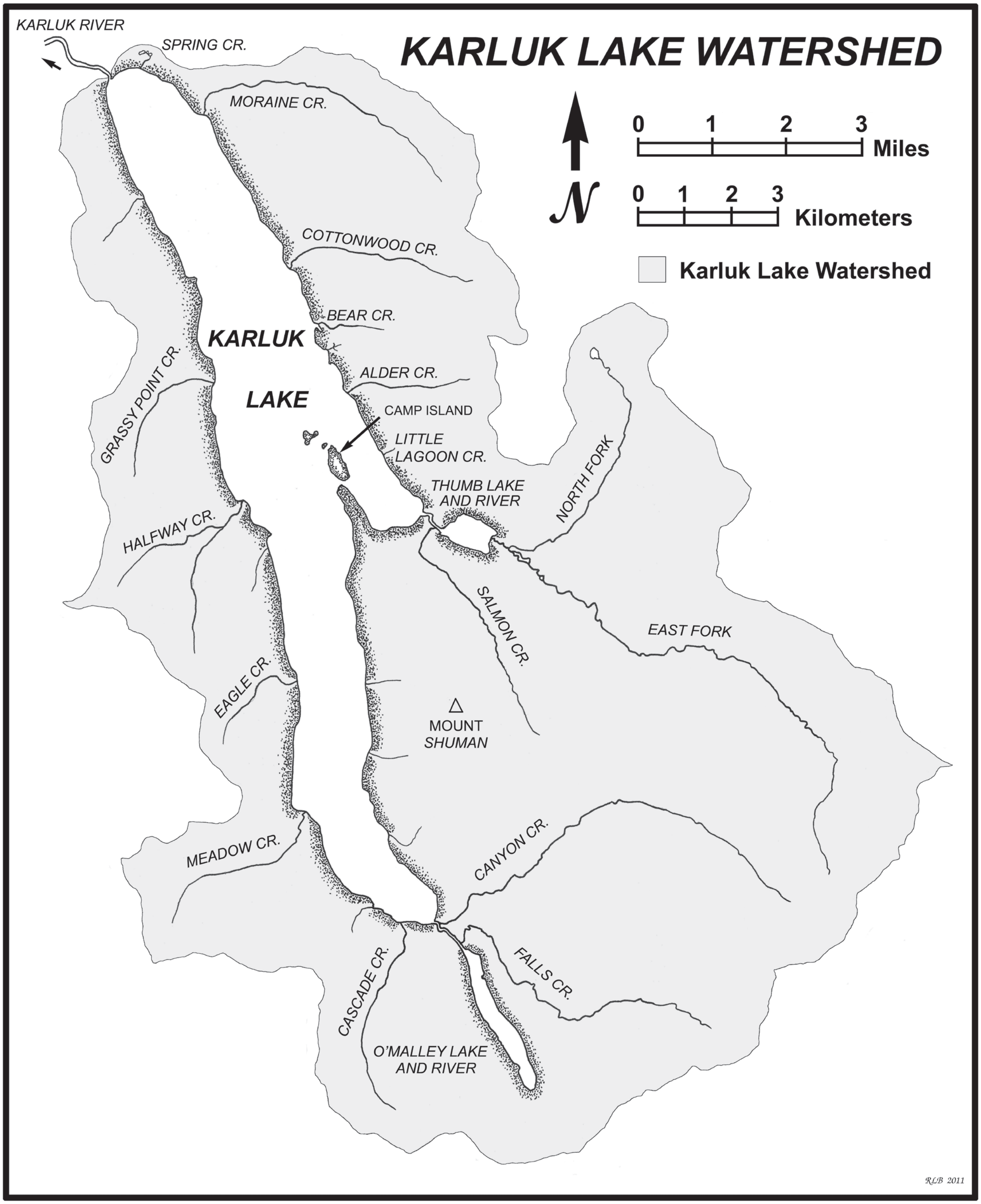


Figure 1-5. Map of the Karluk Lake watershed and tributary streams.

tumbling cascades that restrict spawning salmon to the creeks' lower reaches. In contrast, the two rivers, both with small lakes (Thumb and O'Malley), originate in large tributary valleys, have lower gradients, and provide large spawning areas.

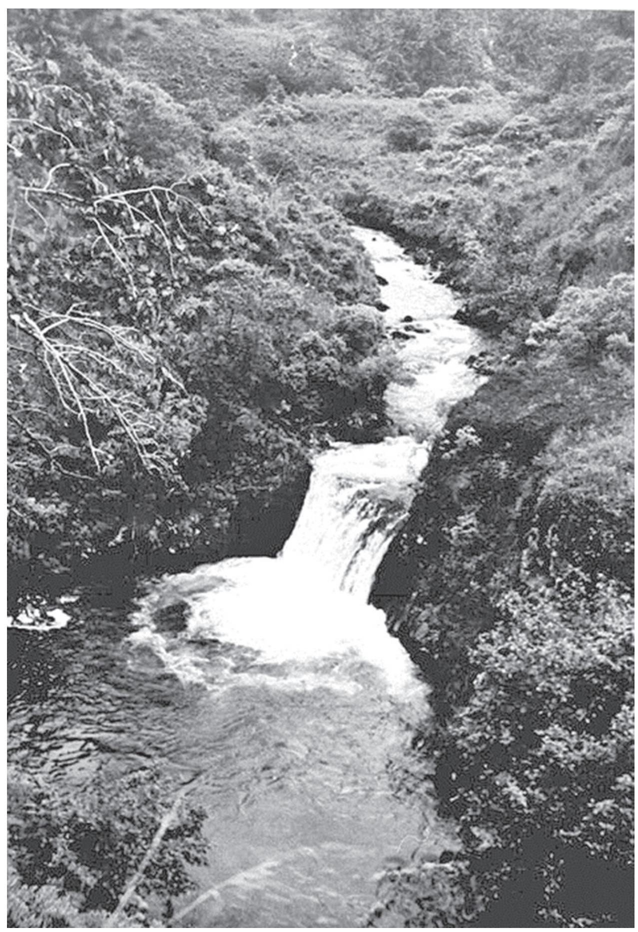
The Karluk River originates at the outlet of Karluk Lake and flows northward and westward 40 km to the ocean at Shelikof Strait. After leaving the lake, the river winds 22 km through a broad valley before turning west through mountainous terrain. Physically, it has a width of 20–160 m and a depth typically less than 1 m. River flow varies seasonally with snowmelt and rainfall runoff—the river's mean discharge is only 12 m^3/sec. The upper 2–4 km of the river is an important spawning area for fall-run sockeye salmon. No barriers to salmon migration exist in the river, except during very dry years when mid summer flows are low; rarely, fish movements are restricted by river ice-cover in early spring. The river enters Karluk Lagoon, a shallow estuary, 5 km upstream from the river's mouth and ocean at Shelikof Strait. Karluk Spit, a 1 km narrow strand beach that rises just a few meters above sea level, separates Karluk Lagoon from the ocean.

For many years Karluk Lake and the upper river were under federal ownership and located within the Kodiak National Wildlife Refuge, which was established in 1941 to protect the island's abundant population of brown bears, *Ursus arctos middendorffi*. Following the Alaska Native Land Claims Settlement Act of 1971, ownership of the Karluk River and northern half of Karluk Lake was transferred to the region's Native groups (the Koniag Corporation).

Eight salmonid species occur in the Karluk ecosystem, including sockeye, pink, coho, Chinook, and chum salmon, steelhead and rainbow trout, Dolly Varden, and Arctic charr (Table 1-1). In addition, threespine stickleback, ninespine stickleback, and coastrange sculpin are present. Though Karluk is renowned for its sockeye salmon, there are also abundant runs of pink

Karluk Lake, showing Island Point (left near), Camp Island (larger island), and Gull Island (smaller island), 1940. (Allan C. DeLacy, from Catherine J. DeLacy, Seattle, WA)

Karluk Lake, with Camp Island in the distance (right center), ca. 1958. (Robert F. Raleigh, Saint George, UT)



Canyon Creek, a salmon spawning tributary at the south end of Karluk Lake, 1948. (Richard F. Shuman, Auke Bay Laboratory, Auke Bay, AK)

North end of Karluk Lake and upper Karluk River, May 1954. (Clark S. Thompson, Shelton, WA)

Lower Karluk River near Alaska Department of Fish and Game salmon counting weir, 1996. (Richard Lee Bottorff, South Lake Tahoe, CA)

Upper Karluk Lagoon, 1996. (Richard Lee Bottorff, South Lake Tahoe, CA)

Karluk River and Karluk Spit salmon canneries, 4 May 1901. (W. C. Fitchie, William J. Aspe Collection, Anchorage Museum, Gift of Mary Rolston, B1990.13.4)

Shelikof Strait (left), Karluk Spit salmon canneries (center), and Karluk River (right), June 1906. (John N. Cobb, University of Washington Libraries, Special Collections, Cobb 2388)

Karluk Lagoon (left), Karluk Spit (center), Karluk Head (upper right), and Shelikof Strait (right), ca. 1953. (Rev. Norman L. Smith, from Timothy L. Smith, Fontana, CA)

Karluk Lagoon (center), Karluk Spit, and Shelikof Strait (left), ca. 1952. (Charles E. Walker, Sechelt, BC)

Karluk Spit and Karluk Lagoon. 1964. (U.S. Fish and Wildlife Service, National Digital Library)

Shelikof Strait (left), Karluk Spit (center), and Karluk Lagoon (right), 1990. (Jet Lowe, Library of Congress, Historic American Buildings Survey, AK, 12-KARLU, 1-1)

salmon during even-numbered years, when several million of them can return to the river. The Karluk River has good runs of coho salmon, Chinook salmon, and steelhead, each of these typically numbering from a few thousand to several tens of thousands of fish annually. Interestingly, only a few hundred chum salmon return to the Karluk River each year, in contrast to major runs that enter the nearby, lake-free Sturgeon River.

Sockeye Salmon

The anadromous life cycle of Karluk's sockeye salmon takes place in two aquatic habitats—the marine waters of the North Pacific Ocean and the fresh waters of Karluk Lake. Each year, mature adults return from the ocean to spawn in their natal fresh waters in and around Karluk Lake. To reach the lake, the salmon ascend 40 km of the Karluk River from the ocean, this upstream migration taking from one to several weeks. Eggs deposited in spawning gravels over-winter there and hatch into young sockeye (known as alevins while they still have an egg yolk sac). In the early spring and summer, these young fish (now known as fry, 24–30 mm long) emerge from the gravel and migrate to Karluk Lake, first feeding for a few months in the shallow shore zone (the littoral) before moving further offshore into the open-water limnetic zone. After rearing in Karluk Lake for two to three years, the juvenile sockeye (now called smolts, 100–150 mm long) make their spring migration to the ocean, where they feed and grow for another two to three years before returning to the Karluk River as mature adults. During their ocean life in the Gulf of Alaska and Bering Sea, Karluk's sockeye migrate thousands of kilometers from their natal river. At maturity, Karluk's sockeye salmon measure about 500–600 mm in length and weigh about 2–3 kg. Typically, the most abundant age group of sockeye salmon adults at Karluk is labeled as 5_3 (or 2.2 in another aging system), meaning that their total age is 5 years between egg deposition and adult spawning, with 3 of these years spent in freshwater as an egg and juvenile before the smolts migrate to the ocean. For the 5_3 sockeye salmon, juveniles rear for two years in Karluk Lake and two years in the ocean before returning to the river as mature adults

Adult sockeye salmon in ocean colors, Karluk Spit beach, 1956. (John Q. Hines, Mt. Shasta, CA)

Male sockeye salmon in spawning colors, Karluk River weir, 1970. (Benson Drucker, Reston, VA)

(the Appendix describes the many different life cycles of Karluk's sockeye salmon). Age groups 6_3 (2.3) and 6_4 (3.2) are also common, and in some years these categories are abundant or dominant components of the run. The colors of adult sockeye salmon change from bright silver-blue in the ocean to vivid red and green when spawning in freshwater. Sockeye salmon adults die within a few weeks of spawning.

Compared with other species of Pacific salmon that occur in Alaska, sockeye salmon possess several unique characteristics. First, sockeye salmon almost invariably return to spawn in river systems that have an upstream lake, the juveniles rearing in this lacustrine habitat for several years before returning to the ocean. Second, the annual return of adult sockeye to a river system is composed of over 20 different combinations of freshwater and ocean ages. That is, juvenile sockeye can spend anywhere from zero to four years feeding in their nursery lake, followed by zero to five years in the ocean before returning to spawn in their natal freshwaters. Thus, compared with other salmon species, the life cycle of sockeye salmon is rather complex. A third unique characteristic is that sockeye salmon have distinctive morphological, physiological, and behavioral adaptations in their life cycle and feeding habits. Both juvenile and adult sockeye salmon have long, fine gill rakers along the inner edge of their gill arches that let them capture small planktonic foods in the limnetic or pelagic waters of the lake or ocean. Hence, sockeye salmon feed at a somewhat lower trophic level than other salmon species. Sockeye salmon also differ from other salmon species in their schooling behavior. It took biologists many years to fully understand the uniqueness of sockeye salmon.

Karluk's sockeye salmon possess another extraordinary biological feature—the ability to modify the productivity of their freshwater nursery lake and the growth and survival of their young. Although this capacity is not yet fully understood, juvenile sockeye benefit via the food chain from nutrients released into the lake when adult salmon die and their bodies decompose. This nutrient interaction between adults and juveniles provides an important insight into at least one controlling mechanism of sockeye salmon in freshwater. Further, this ability to transform the environment of their nursery lake strongly suggests that sockeye salmon are keystone species in the Karluk ecosystem, directly and indirectly influencing a wide range of the region's fauna and flora.

Although Karluk is renowned for its many sockeye salmon, another remarkable aspect of these runs is their long seasonal duration. Adult sockeye first enter the Karluk River in late May and continue throughout most of the summer and early autumn. Two peaks of abundance occur, one in June and a second in early August or September. Typically, the runs decline by late September, but they can extend into October, and more rarely, into November. Sustained large runs of sockeye salmon in August–September are uncommon in other river systems of Kodiak Island and southwestern Alaska. The extended run duration at Karluk was an attractive biological feature for the commercial fishery and canneries to exploit.

Purpose

The main purpose of this book is to review the more than 100 years of fisheries research on Karluk River sockeye salmon. We have summarized and integrated the large mass of research data that has been collected on many complex, dynamic, and interrelated biological topics. This research history is interesting and revealing because it spans the years when knowledge about sockeye salmon grew from near complete ignorance about its life history and biology in 1880, to a relatively detailed understanding in 2010. Scientific facts about salmon accumulated rather slowly before 1900, but discoveries quickened after the foundations and techniques of the new discipline of fishery biology developed.

Over the past century, a long succession of biologists have studied many aspects of Karluk's sockeye salmon and published their findings in scientific journals or agency reports. Yet, many significant results have remained unpublished and unknown to other researchers. This deficiency has obscured a more complete biological understanding of sockeye salmon and caused later biologists to unknowingly repeat previous studies. Thus, in this comprehensive review of sockeye salmon research at Karluk, we have tried to clearly present what has been done and where the original data exists for both published and unpublished studies. While this review demonstrated that substantial knowledge now exists about sockeye salmon, it also revealed that important biological questions remain.

Throughout this review we used the term "Karluk" as an abbreviated way to designate the whole Karluk River and Lake ecosystem. When greater specificity was needed we used the following geographic terms, proceeding upstream from the ocean—Karluk Spit, Karluk Village, Karluk Lagoon, Karluk River, Karluk Portage, and Karluk Lake (Fig. 1-4).

A central theme of this research history is the scientific controversy that arose about the fundamental cause(s) of the long-term decline and subsequent recent recovery of sockeye salmon abundance at Karluk. Many well-known fishery biologists of the 1900s discussed and promoted at least 12 different theories to explain these population trends: 1) overfishing of the entire run, 2) reduced lake fertility, 3) asynchrony of plankton blooms and fry emergence, 4) overfishing of productive midseason subpopulations, 5) environmental changes, 6) reduced reproductive capacity, 7) charr predation on juvenile sockeye, 8) brown bear predation on adult sockeye, 9) counting weir impediments to salmon migrations, 10) competition between juvenile sockeye and sticklebacks, 11) operation of the Karluk Lagoon hatchery in 1896–1916, and 12) interaction between ocean climate and lake fertility.

As fisheries research continued at Karluk over many decades, certain theories gained prominence for a time, only to be replaced by other ideas as new data were analyzed. Some theories that initially were widely accepted fell into disfavor, but later regained prominence. Because the search for the correct theory has been such a prominent part of Karluk's fisheries history, much of this book is organized around these theories, with different aspects of the scientific debate being reviewed in separate chapters.

It should be clearly stated, however, that biologists still do not fully understand the controlling factors of Karluk's sockeye salmon abundance, and it is likely that additional theories and explanations will be proposed in the future. The difficulty of settling on a theory is a result of the inherent complexity of sockeye salmon and its environment—this includes marine and freshwater life stages, ocean climate regimes, marine and lake water temperatures, upwelling areas, nutrients, primary production, plankton, variable foods, competing species, multiple predators, diseases, parasites, long migrations, multiple age classes, size variations, and subpopulations. And beyond the numerous natural factors, there is the impact of commercial harvests. Predicting the outcome of such a diverse and complex system requires a large dose of humility. For that reason, we do not disparage any of the proposed theories to explain the abundance of Karluk River sockeye salmon. All were originally formulated after due consideration of then available facts and with the notable goal of sustaining this salmon resource.

An important goal of this project was to prepare a useful historical and biological resource for biologists, fishery managers, historians, fishermen, naturalists, and Alaskan enthusiasts that summarizes the many years of research on Karluk River sockeye salmon. Besides the many people and organizations directly involved in sockeye salmon research and management in Alaska, we sense that the Karluk River system engenders keen interest from biologists worldwide because of the early prolific runs, long-term decline and recent rebound, and many years of research.

Thus, we have attempted to provide a comprehensive review of past sockeye salmon research at Karluk, access to the full range of research literature, a description of a fascinating period of Alaska's history, and suggestions for future research. Our goals will be partially realized if past studies at Karluk can be readily identified and future research can avoid unnecessary duplication. Of course, we hope this book will ultimately lead to an even greater understanding of Karluk's sockeye salmon and to the perpetuation of abundant and healthy runs of this adaptable and resilient salmon in a magnificent river-lake ecosystem of Alaska.

Report Organization

This research history is divided into 11 chapters that summarize and discuss many important topics of sockeye salmon research at Karluk. First, we chronologically review the research efforts and discoveries of nearly 20 biologists who studied Karluk's sockeye salmon during the 90 years between 1880 and 1970 (Chapter 2). Fisheries research during this era was conducted by a series of naturalists, biologists, and ichthyologists of the U.S. Government, primarily from its U.S. Fish Commission (USFC), Bureau of Fisheries (USBF), Fish and Wildlife Service (FWS), and Bureau of Commercial Fisheries (BCF). Additional research was conducted during the latter part of this era by biologists from other organizations, including the Fisheries Research Institute (FRI) of the University of Washington, Seattle; the Alaska Department of Fisheries (ADF) before statehood; and the Alaska Department of Fish and Game (ADFG) after statehood.

Second, we review the history of the Karluk River counting weir, from its first operation in 1921 to current times (Chapter 3). This fisheries research tool has provided a wealth of basic data on sockeye salmon escapements (the number of fish that escape the fishery and reach the spawning grounds), migration timing, and run composition, as well as similar facts for other salmonid species that inhabit the system. The weir history

is interesting because of its various operational problems, the long-term debate over its proper location, its changing uses, and the insights it provided into the dynamism of the Karluk River ecosystem.

Third, we summarize the life history of Karluk's sockeye salmon (Chapter 4). Compared with the little that was known about this species in 1880, a substantial amount has been learned over the decades. Nevertheless, some important details of its life history still remain unclear and continue to be topics for future study.

Following these initial chapters that summarize information across many fishery subjects, the next six chapters (Chapters 5–10) provide detailed reviews of specific topics, controversies, and questions that have persisted about sockeye salmon throughout most of Karluk's research history: 1) the existence of subpopulations, 2) the seasonal run distribution, 3) the importance of limnological knowledge and lake fertilization, 4) the interaction of sticklebacks and juvenile sockeye, 5) the effect of charr predation, and 6) the effect of bear predation. To summarize and conclude the central theme of this book, the final chapter (Chapter 11) briefly reviews the different theories that have been proposed to explain the historic decline and recent recovery of sockeye salmon runs at Karluk. In all chapters, we trace the origin and historical development of thought about each major topic and conclude with a statement of the current understanding.

Supporting this historical review of sockeye salmon research at Karluk are two major supplements: 1) an appendix of long-term fisheries data and biological resources, and 2) a comprehensive bibliography (published as a companion volume). The appendix includes the daily weir counts of sockeye salmon from 1921 to 2010, plus a gazetteer, glossary, timeline, summary of management reports, scale resources, life cycle and age composition graphs, and summary of biotic resources. The bibliography includes both published and unpublished references on Karluk's sockeye salmon, in addition to many citations on the region's fauna, flora, history, and physical environment. Most references have been annotated to quickly reveal their contents. We have tried to include all Karluk references up to 2010.

Throughout this book, we have included many historical images of the research gear, weir, personnel, facilities, scenery, fauna, and flora. We believe the historical photographs give clear insights into the many years of field studies and reveal what for many biologists was a stimulating research experience and an exciting Alaskan adventure.

This history of sockeye salmon research at Karluk complements, but has little overlap with, previous histories of the salmon canneries of Kodiak Island and the salmon hatcheries of Alaska by Patricia Roppel (1982, 1986). Since Roppel has admirably discussed these two subjects, we have not repeated her work, except to occasionally add specific information about Karluk.

Sources of Information

This research history is based upon many primary and secondary sources of published and unpublished information. Without a doubt, the number of pertinent references that we discovered far exceeded our initial expectations. We focused our literature search on the biology of Karluk's sockeye salmon, but we also gathered literature on other species of its fauna and flora, the physical environment, and the fishery. Published references included those in peer-reviewed journals and fishery agency reports, while unpublished documents were found in various libraries, archives, and personal collections. Within the time constraints of this project, we believe that a major portion of Karluk's fisheries literature was examined, especially for the pre-statehood period of Alaska. Although the Bare Lake study of the 1950s was an offshoot of the Karluk research program, we did not thoroughly examine this literature. The results of our literature search are presented in the Karluk Sockeye Salmon Bibliography.

To supplement our literature search, we directly interviewed many active and retired biologists, all of whom conveyed valuable insights into the Karluk ecosystem and the past and current research programs. They discussed technical facts about sockeye salmon and recalled biological studies from as far back as the 1930s. Overwhelmingly, these biologists were highly enthusiastic about the Karluk ecosystem and their own research experiences there. Further, many biologists supplied us with personal photographs taken during their years of field work at Karluk; these images added considerable detail about past field studies, facilities, and personnel.

As the Karluk references were gathered, we chronologically organized the published and unpublished information into a large computer database that included about 90 biological, fisheries, historical, and other topics. Most subjects dealt with some aspect of sockeye salmon biology, but some computer files summarized data on the physical, historical, archeological, and other biological properties of Karluk. Besides sockeye salmon,

the database included information on a broad spectrum of the flora and fauna—all fish species, aquatic invertebrates, parasites, birds, mammals, and plants. Though not all of these topics were included in our subsequent review, this database provided a broad foundation for the discussion of Karluk's sockeye salmon.

As we reviewed the past research and interacted with many biologists, one fact became exceedingly clear—the dynamic nature of the Karluk lake-river ecosystem. Its sockeye salmon, plus many other of its fish and wildlife species, undergo large seasonal changes in abundance and distribution. For its fishes, each life stage is often associated with a major migration among different habitats, either between freshwater and the ocean or within the lake and its tributaries. Likewise, the aquatic habitats experience large seasonal variations in their physical and chemical properties. We emphasize the dynamic nature of the Karluk ecosystem because it adds an important overriding qualification to most research programs. That is, only by collecting samples over a wide range of places and times can the full complexity of many biological phenomena be understood. Sometimes in the past, research conclusions have been incorrectly extrapolated from a few measurements of location and season. Because of the inherent dynamism that defines the Karluk system, we have attempted in this history to clearly specify the times and places when discussing biological topics about sockeye salmon.

Wonderful Karluk

We close this introduction with a group of historical comments about the original productivity and uniqueness of the sockeye salmon runs in the Karluk River. Visitors to Karluk between the 1880s and the early 1900s marveled at these bountiful runs, a magnificent cornucopia of silver fish that arrived from the sea and flowed upriver with tenacious force for months on end. Documents from this period, and somewhat later, often included glowing reports about the "wonder of the Karluk sockeye salmon runs." The following quotations demonstrate the special attraction that this remarkable salmon species and Karluk ecosystem have had for many people:

> [Speaking of Karluk's salmon, 1880] Looking down into the water, it would seem that a lead-pencil could not be passed down between the densely crowded fish; a bidarka cannot be paddled over them when the salmon are thick. Red salmon are abundant every year at Karluk. [Bean, 1887: 96]

> [1889] The run is confined chiefly to the smaller streams, such as the Karluk, in which they crowd in numbers absolutely incredible to one who is not an eye witness, and actually force each other out of the water in their eager struggles to reach the sources of the rivers and deposit their spawn. [Bean, 1891: 168]

> [1889] The number of salmon actually caught in Karluk Bay, near the river mouth and in the lower portion of the river, is so large as to make a true statement concerning them seem incredible. In 1888 the canneries put up over 200,000 cases, averaging about 13 red salmon to the case, or more than 2,500,000 fish. In 1889 the number of fish put up was still larger, reaching probably 250,000 cases, containing more than 3,000,000 salmon. [Bean, 1891: 182]

> [1890] The Karluk river became known to the Russians as the most prolific salmon stream at an early date, and they utilized it as a depot for supplying their numerous hunting parties with dry fish as early as 1793. Ever since that time that wonderful little river has been made to yield its annual quota for the subsistence of Alaskan people. [Porter, 1893: 79]

> [1890] You see, the best fishing of all was right there at Karluk at the seining grounds. I thought I'd seen fish down on the Columbia and in at the mouth of the Fraser River, but I never seen fish anywhere to equal them runs at Karluk. We'd bring in twenty-five to thirty thousand big salmon in a haul. [McKeown, 1960: 42]

> [1895] It is unusual for more than one establishment to be found on any salmon stream, but at Karluk . . . there are five canneries, and the salmon seem inexhaustible. The river at its mouth, and for a long distance out into the salt water . . . seems to be fairly swarming with these fish. They fill the water to such extent as to almost dam it up, and those below, in their eagerness to ascend the river, crowd those on top so that their fins and part of their body are exposed to view. The first season I beheld the sight I though an appropriate name would be the "River of Life". [Bruce, 1895: 40]

> [1897] In 1896 several hauls on Karluk Spit yielded 75,000 salmon to the haul. Hauls of from 25,000 to 30,000 fish are not unusual during the height of the run. It is said that some years ago 100,000 salmon were taken at a single haul on the spit. . . . The waters surrounding the outlet to Karluk Lagoon are probably the most remarkable in salmon production in Alaska, not only in point of numbers, but in the length of the runs. [Moser, 1899: 145–146]

> [1903] The four greatest of red salmon streams are the Fraser River, Karluk River, Nushegak River and Kvichak River, all large streams flowing through lakes. In

proportion to the amount of water, probably no stream in the world normally carries more salmon than the Karluk River. [Jordan, 1903: 171]

[Speaking of Karluk, 1909] When the salmon runs began there were so many fish that they almost pushed each other out of the water. When we went out in rowboats it sounded like someone beating a tattoo on the bottom of the boat, we had to pole because the fish were so thick you couldn't get the oars down to row. [Taylor 1964: 36]

[At the Karluk River, 21 July 1916] This was the first time I had seen the river above the hatchery. It is easy to understand why the Karluk River has been such a wonderful salmon stream. As a breeding ground for salmon, it so far surpasses anything that I have seen in Alaska as to be entirely in a class by itself. Conditions, as observed by me in a very limited time and over a small area as compared with the whole, are perfect and ideal in every respect. [Ball 1916]

[Speaking of Karluk, 1931] Although other species are taken in the fishery the remarkable red-salmon runs are of predominant importance. Both the river and the lake are relatively small, yet the abundance of red salmon is so great as to indicate that conditions are particularly favorable for this species. No other stream of similar size is known to produce such large runs, and there are only a few larger streams, such as the Fraser and the Kvichak Rivers, that have been more productive. . . . The history of this district is particularly interesting, and marks the rise and fall of one of the world's greatest red-salmon fisheries. [Rich and Ball 1931: 664–665]

[Speaking of Karluk, 1932] This watershed, for it size, has been one of the greatest producers of red-salmon in the world. [Barnaby 1932: 1]

[Speaking of Karluk, 1958] That night I lay in the forward bunk listening to the gurgle of the mighty Karluk as it bubbled against the port planks. I wondered if people appreciated what this great river had meant to them in the past as they casually reached for a can of red salmon on a grocery shelf in New York or Austin. Karluk, the river of giants, where bloody wars were once fought over the right to fish for the fresh-run horde as they piled in from the Shelikoff Straits by the thousands, only to die in the spawning beds of Karluk Lake where their decaying bodies produced the plankton so vital as food for the fingerlings. . . . But these great salmon runs into the Karluk River are a thing of the past and only a trickle remains. For years commercial fishermen exploited the big fish, and protective laws were passed too late. [Woodworth 1958: 105]

[Speaking of Karluk, 1971–1972] Karluk Lake is the largest lake . . . on Kodiak Island and historically supported a sockeye run of greater magnitude, in relation to lake size, then any other sockeye producing system in the world. [Blackett 1973: 70]

As these statements confirm, most visitors to Karluk, whether professional biologists, officials, laborers, sportsmen, or tourists, soon grasped the exceptional nature of this river-lake ecosystem and its abundant sockeye salmon runs. Indeed, a near reverence for these fish and the wild setting soon permeates those who visit or study the Karluk system, the admiration flowing from diverse sources—from seeing the bold natural landscape, clear waters, and persistent salmon masses; from understanding the extended evolutionary history that adapted these salmon to flourish in this river system; from appreciating the long human prehistory and

Bidarka on Karluk River (near), Karluk Spit cannery buildings, and steamers *Bertha* and *Haytien Republic* in Shelikof Strait (far), 1889. (Tarleton H. Bean, National Oceanic and Atmospheric Administration Photo Library, fish7460, from National Archives, Washington, DC)

varied fisheries history that unfolded on these now quiet shores; from knowing the 100-year succession of biologists who worked to unlock the secrets of sockeye salmon; and from experiencing a powerful connection with untamed nature. Nowadays, such sentiments come from people of many backgrounds, interests, and origins, the enthusiasm being particularly ardent from worldwide visitors that travel long distances to sport fish for Karluk's salmon, steelhead, and charr and to experience a unique adventure in an intact Alaska wilderness. Clearly, whether viewed from the perspectives of modern ecological principles and sensibilities or of Alaskan history, the sockeye salmon runs at Karluk are a remarkable phenomenon.

Photo Supplement

This supplement to Chapter 1 presents a photo collection of salmon can labels, wooden crates, and a cannery company logo. These items were used by historic salmon canneries that harvested and canned Karluk River sockeye salmon.

Selected Salmon can label, put up by Karluk Packing Co., Karluk, Kodiak Island, Alaska. (Ralph and Terry Kovel, *The Label Made Me Buy It,* Crown Publishers, NY, 1998)

Selected Salmon can, put up by Karluk Packing Co., Karluk, Kodiak Island, Alaska. (Karen Hofstad Collection, Petersburg, AK)

Karluk Packing Co. sockeye salmon crate, Horse Shoe Brand, Alaska Packers Association, San Francisco. (National Park Service, San Francisco Maritime National Historical Park, San Francisco, CA, SAFR 19302)

Horse Shoe Brand salmon can label, Karluk red salmon, Alaska Packers Association, San Francisco. (Courtesy of the Pratt Museum, Homer, AK, 2004 [label image], and Captain Richard C. Sturgill, Drayton Harbor Maritime and Alaska Packers Association Museum, Blaine, WA [APA trademark])

Canoe Brand salmon can label, packed by Alaska Improvement Co., Karluk, Alaska. (Ralph and Terry Kovel, *The Label Made Me Buy It,* Crown Publishers, NY, 1998)

El Modelo Brand salmon can label, spring catch Alaska salmon, packed by Alaska Improvement Co., Karluk, Alaska. (Lantern Press, Seattle, WA)

Canoe Brand salmon can label, Alaska red salmon, packed by Alaska Packers Association, Karluk, Kodiak Island, Alaska. (Warren E. "Nick" Nickell, Vancouver, WA [label image], and Captain Richard C. Sturgill, Drayton Harbor Maritime and Alaska Packers Association Museum, Blaine, WA [APA trademark])

Kodiak Brand salmon can label, packed by Aleutian Islands Fishing & Mining Co., Kodiak Island, Alaska. (Lantern Press, Seattle, WA)

Kodiak Brand salmon can, Alaska red salmon, packed at Karluk, Alaska Packers Association, San Francisco, successors to Aleutian Island Fishing & Mining Co. (Karen Hofstad Collection, Petersburg, AK)

Alaska Packers Association headquarters plaque and logo, San Francisco. (National Park Service, San Francisco Maritime National Historical Park, San Francisco, CA, SAFR 20963 [plaque image], and Captain Richard C. Sturgill, Drayton Harbor Maritime and Alaska Packers Association Museum, Blaine, WA [APA trademark])

Coleman Flag Brand salmon crate, Alaska red salmon, packed at Kodiak Island, Alaska, by Alaska Packers Association. (Alaska State Museum, Juneau, AK, ASM 2005-20-1)

Cape Karluk Brand salmon can, Alaska red salmon. (Alaska State Museum, Juneau, AK, ASM 91-45-2)

Hume's Karluk Brand salmon can, Alaska red salmon, Hume Packing Co., at Karluk, Alaska. (Alaska State Museum, Juneau, AK, ASM 2002-13-1 [can image], and Captain Richard C. Sturgill, Drayton Harbor Maritime and Alaska Packers Association Museum, Blaine, WA [APA trademark])

Hume's Karluk Brand salmon crate, Alaska red salmon, packed by Alaska Packers Association. (Captain Richard C. Sturgill, Drayton Harbor Maritime and Alaska Packers Association Museum, Blaine, WA)

Rocky Point Brand salmon can label, spring pack Alaska salmon, packed by Hume Packing Co, at Karluk, Alaska. (Warren E. "Nick" Nickell, Vancouver, WA)

Hume's Karluk Brand salmon can label, red salmon, Alaska Packers Association, San Francisco. (Richard Lee Bottorff, South Lake Tahoe, CA [label image], and Captain Richard C. Sturgill, Drayton Harbor Maritime and Alaska Packers Association Museum, Blaine, WA [APA trademark])

Aurora Borealis Brand salmon can label, Alaska red salmon, Arctic Packing Co., Karluk, Alaska Packers Association, San Francisco. (Lantern Press, Seattle, WA [label image], and Captain Richard C. Sturgill, Drayton Harbor Maritime and Alaska Packers Association Museum, Blaine, WA [APA trademark])

Russian American Brand salmon can label, Alaska red salmon, put up by the Russian American Packing Co., Karluk, Alaska Packers Association, San Francisco. (Lantern Press, Seattle, WA [label image], and Captain Richard C. Sturgill, Drayton Harbor Maritime and Alaska Packers Association Museum, Blaine, WA [APA trademark])

Gold Medal Brand salmon can label, fresh red Alaska salmon, Kodiak Packing Co., packed by Alaska Packers Association, Karluk, Alaska. (Lantern Press, Seattle, WA [label image], and Captain Richard C. Sturgill, Drayton Harbor Maritime and Alaska Packers Association Museum, Blaine, WA [APA trademark])

Seward Brand salmon can, Alaska red salmon, packed at Karluk, Alaska Packers Association, San Francisco. (Karen Hofstad Collection, Petersburg, AK)

Seward Brand salmon crate, Alaska red salmon, packed at Karluk by Alaska Packers Association. (Maine Maritime Museum, Bath, ME [crate image] and Captain Richard C. Sturgill, Drayton Harbor Maritime and Alaska Packers Association Museum, Blaine, WA [APA trademark])

Cruiser Brand salmon can, Alaska salmon, packed at Karluk, Alaska Packers Association, San Francisco. (Karen Hofstad Collection, Petersburg, AK [can image], and Captain Richard C. Sturgill, Drayton Harbor Maritime and Alaska Packers Association Museum, Blaine, WA [APA trademark])

Pioneer Fishery salmon can label, Karluk red salmon, Hume Bro's & Hume's, Pacific Packing & Navigation Co., New York, San Francisco, Seattle. (Karen Hofstad Collection, Petersburg, AK)

Peerless Brand salmon can label, Karluk red salmon, packed by Hume Brothers and Hume, Uyak Bay, Alaska. (Warren E. "Nick" Nickell, Vancouver, WA)

Little Commodore Brand salmon can label, Karluk red salmon, packed by Hume Brothers and Hume, Uyak Bay, Alaska. (Warren E. "Nick" Nickell, Vancouver, WA)

Primer Brand salmon can label, Karluk red salmon, packed by Hume Brothers and Hume, Uyak Bay, AK. (Warren E. "Nick" Nickell, Vancouver, WA)

Karluk Primer Brand salmon can label, Alaska red salmon, Hume Bro's & Hume's, packed by Northwestern Fisheries Co., Seattle. (Warren E. "Nick" Nickell, Vancouver, WA)

CHAPTER 2

Karluk Sockeye Salmon Research History

Nature does not reveal all her secrets at once . . .
Of one of them this age will catch a glimpse,
of another, the age that will come after.—L. A. Seneca, AD 64

When the United States purchased Alaska from Russia in 1867, little had been written about any Karluk River salmon, especially concerning details of life history. Even the most basic biological facts remained mysteries to the scientific community. Yet, because Karluk River salmon had been important subsistence resources for the indigenous Alutiiq people of Kodiak Island for many thousand years, these early inhabitants must have accumulated considerable knowledge about the river and its different fish species.

Many Alutiiq were attracted to the Karluk River because of the abundant salmon runs that returned at predictable times each year. These fish were annually harvested, dried, and stored as a vital food source, rich in energy and nutrients, which sustained the early inhabitants for many months. Since their survival was directly linked to these salmon, the Alutiiq closely observed the kinds, abundance, and timing of fish migrations that entered the river each year. This accumulated wisdom was passed to succeeding generations by oral and cultural traditions.

Karluk River salmon also were important food resources for the Russian fur traders during 1784–1867. At least rudimentary knowledge about the fish species present and timing of the runs was needed to harvest the salmon, but little of this information was formally documented. Fragmentary insights about Karluk River salmon can be found in official reports of the Russian–American Company, but, in general, these only tallied the number of fish dried as food for local use or by sea otter hunting crews. Almost nothing was written about the salmon's biology. Often these early reports were based on brief visits to Karluk by company officials or from conversations with the employees who actually caught and dried the salmon. Naturalists aboard several Russian voyages of exploration and official visitors to Kodiak Island during 1784–1867 often mentioned the region's abundant fishery resources, but they seldom wrote specifically about Karluk's salmon.

Several individuals and companies commercially harvested and salted or dried salmon at the Karluk River during 1867–81 and sold their products in Kodiak Island and west coast markets. These initial commercial ventures, though of limited scale and success, required some knowledge about Karluk's salmon, but again little biological information was ever published.

The first commercial cannery began operations on Karluk Spit in 1882, initiating many decades of large harvests of its sockeye salmon. The huge runs and long harvest season made this an attractive resource to exploit, and the number of canneries that took fish from the Karluk River rapidly expanded. Sockeye salmon were harvested with beach seines that were made longer each year and more capable of catching many thousands of fish in a single haul. Soon, the federal government grew concerned that the ever-increasing harvests threatened the salmon's long-term survival. Consequently, early during this fishery, the federal government began to study these sockeye salmon to understand the biological processes sustaining abundant and healthy runs, though the inherent complexity of this species and its environment was not fathomed for many years. Most biological investigations of Karluk River sockeye salmon since 1882 have been focused on the long-term goal of assuring sustainable and healthy runs.

In this chapter, we trace the development of biological knowledge about Karluk River sockeye salmon from 1880, when essentially nothing was known about its life history, to 1970, when much was known.[1] Our chronological discussion is organized around the many biologists who successively studied sockeye salmon at Karluk (Table 2-1; Fig. 2-1). We ended the research history in 1970 because in that year the U.S. government

[1] The U.S. Senate hearing testimony of 1912 gives particularly revealing and detailed insights into the deficiencies of knowledge about sockeye salmon at Karluk and other locations in Alaska and the Pacific Coast (U.S. Senate, 1912).

Table 2-1
Historical outline of fisheries research in the Karluk River basin, 1880–1970.

U.S. Fish Commission
- Tarleton H. Bean (1880, 1889)
  - Descriptions of sockeye salmon runs and harvests in 1880, prior to any cannery operations.
  - Descriptions of sockeye salmon runs and harvests in 1889, after eight years of cannery operations.
  - Reconnaissance survey of the Karluk Lake spawning grounds (1889).
  - Observations of sockeye salmon and other fishes in Karluk Lake and River.
- Cloudsley L. Rutter (1896–97, 1903)
  - Sockeye salmon egg and fry culture at Karluk River Hatchery (1896–97).
  - Reconnaissance survey of Karluk Lake spawning grounds.
  - Observations of sockeye salmon life history at Karluk Lake and River.
  - Travel time of adult sockeye salmon from Karluk Lagoon to Karluk Lake.
  - Dolly Varden food habits.
  - Adult and juvenile sockeye salmon food habits in the ocean.
  - Adult ripening period in Karluk Lake before spawning.
  - Migratory behavior of adult and juvenile sockeye salmon.
  - Detailed count of sockeye salmon spawning in Moraine Creek.
  - Abundance and kinds of wounds received in the ocean by sockeye salmon adults.

U.S. Bureau of Fisheries
- Charles H. Gilbert (1919–27)
  - Reconnaissance of Karluk Lake spawning grounds (1919, 1921–22).
  - Karluk River weir established in 1921.
  - Escapement and total run of sockeye salmon.
  - Seasonal distribution of sockeye salmon run.
  - Freshwater and ocean ages of sockeye salmon determined by reading scales.
  - Seasonal changes in age composition of the adult sockeye salmon run.
  - Stock-recruitment relationship for sockeye salmon.
- Willis H. Rich (1922, 1926–32)
  - Sockeye salmon smolt-to-adult ocean survival and total outmigation numbers (1926–30).
  - Smolt age and lengths of sockeye salmon.
  - Karluk Lake bathymetric map (1926).
  - Limnological sampling at Karluk Lake (1926–30).
  - Influence of salmon carcass nutrients on Karluk Lake productivity.
  - Spawning surveys of sockeye salmon in Karluk Lake and tributaries (1922, 1926–30).
  - Tagging sockeye salmon to determine ocean migration routes along west coast of Kodiak Island (1927).
- J. Thomas Barnaby (1930–38)
  - Sockeye salmon smolt-to-adult ocean survival, by recovery of marked fish (1930–36).
  - Smolt age and lengths of sockeye salmon.
  - Relation between sockeye salmon growth and scale size.
  - Limnological studies of Karluk Lake.
  - Dolly Varden and Arctic charr food habits (1935–36).
  - Dolly Varden and Arctic charr migrations, by tagging (1937–38).
  - Spawning surveys of sockeye salmon in Karluk Lake and tributaries.
- Allan C. DeLacy (1937–42)
  - Dolly Varden and Arctic charr food habits (1939–41).
  - Dolly Varden and Arctic charr migrations, by tagging (1937–42).
  - Dolly Varden and Arctic charr taxonomy and life history (1939–41).
  - Sockeye salmon subpopulation measurements (1939–42).
  - Fecundity of sockeye salmon (1938–41).
  - Limnological studies of Karluk Lake.
  - Food habits of mergansers (1942).
- William M. Morton (1939–42)
  - Discovery that two species of charr were present in Karluk Lake—Dolly Varden and Arctic charr (1939).
  - Morphological and meristic differences between Dolly Varden and Arctic charr (1939–41).
  - Dolly Varden and Arctic charr food habits (1939–41).
  - Dolly Varden and Arctic charr parasites (1939–41).
  - Parasitological studies of many Karluk fishes, birds, and mammals.

U.S. Fish and Wildlife Service
- Richard F. Shuman (1943–49)
  - Fecundity of Karluk River sockeye salmon (1943).
  - Travel time of adult sockeye salmon from Karluk Lagoon to Karluk Lake, by tagging (1945–46).
  - Lake residence time and migration of adult sockeye salmon from Karluk River weir to spawning habitat, by tagging (1946–48).
  - Bear predation on adult sockeye salmon in two Karluk Lake tributaries (Moraine and Halfway Creeks) (1947–48).
  - Analysis of sockeye salmon escapements and returns, and factors causing decline of runs (1945–51).
  - Limnological studies of Karluk Lake and preparation for lake fertilization (1947–49).
  - Operation of weir at the Karluk River Portage (1943–44). Moved weir to Karluk Lake outlet (1945).
  - Attempt to build permanent two-way weir on the Karluk River (1949).
  - Spawning surveys of sockeye salmon in Karluk Lake and tributaries (1943–49).

Table 2-1 (cont.)

Historical outline of fisheries research in the Karluk River basin, 1880–1970.

Philip R. Nelson (1946–56)
- Travel time of adult sockeye salmon from Karluk Lagoon to Karluk Lake, by tagging (1946, 1953).
- Migration of adult sockeye salmon from Karluk River weir to spawning locations, by tagging (1946–48).
- Bear predation on adult sockeye salmon in two Karluk Lake tributaries (Moraine and Halfway Creeks) (1947–48).
- Limnological studies of Karluk Lake (1947–56).
- Limnological and fertilization studies of Bare Lake (1949–56).
- Stickleback life history in Karluk and Bare Lakes (with John T. Greenbank) (1948–56).
- Sockeye salmon egg studies – seeding density, mortality, and development (1947–54).
- Survival and spawning of gill-net marked sockeye salmon (with Carl E. Abegglen) (1953).
- Spawning surveys of sockeye salmon in Karluk Lake and tributaries (1946–56).

George A. Rounsefell (1951–58)
- Review and analysis of past FWS field research results and publication of paper on the decline of Karluk River sockeye salmon runs (1958).

U.S. Bureau of Commercial Fisheries

John B. Owen (1957–59)
- Review of Karluk River sockeye salmon research and discussion of the factors affecting production, emphasizing subpopulations and differences in spawning time and location (with Charles Y. Conkle and Robert F. Raleigh) (1962).
- Determination of spawning habitat types and seasonal use by sockeye adults.
- Diurnal spawning behavior of sockeye salmon in Karluk Lake tributary streams.
- Survival time of adult sockeye salmon in Karluk Lake tributary streams.
- Spawning pen studies of adult sockeye salmon.
- Sculpin life history study (with John T. Greenbank).
- Dolly Varden food habits study (with John T. Greenbank).
- Physical characteristics of Karluk Lake spawning habitats (substrates and gradients).
- Egg survival studies.
- Limnological studies of Karluk Lake and tributary streams.
- Operation of counting tower on Karluk River (1958–59).

Robert F. Raleigh (1956–61, 1965–66)
- Fertilization studies of Bare Lake (1956).
- Post-fertilization studies of zooplankton (1957), limnology, and sockeye and other fish populations (1957–61).
- Tributary homing of adult sockeye salmon in Karluk Lake, including tenacity of stream preference and effect of conditioning (1959–61).
- Determination of innate migration direction (upstream or downstream) in emergent sockeye salmon fry from the Karluk River and Karluk Lake tributaries (1958, 1965–66).
- Review of Karluk River sockeye salmon research and report on factors affecting production, emphasizing subpopulations and distinct differences in spawning time and location (with John B. Owen and Charles Y. Conkle) (1962, 1969).
- Total outmigration of sockeye salmon smolts determined (1961).
- Subpopulation differences of adult sockeye salmon in different spawning habitats was examined (1959–61).
- Spawning surveys of sockeye salmon in Karluk Lake and tributaries.

Richard Gard (1962–66)
- Travel time of adult sockeye salmon from Karluk River Portage to Karluk Lake (1963).
- Bear predation on adult sockeye salmon in a Karluk Lake tributary (Grassy Point Creek) (1964–65).
- Detailed spawning study and survival of sockeye salmon of Grassy Point Creek.
- Total freshwater and marine survival of Karluk River sockeye salmon.
- Subpopulation determination of sockeye salmon in Karluk Lake and its tributaries (1962–66).
- Relationships between fecundity and sockeye female size in many Karluk spawning habitats.
- Total outmigration of sockeye salmon smolts determined (1962–66).
- Merganser food habits at Karluk Lake (1965).
- Spawning surveys of sockeye salmon in Karluk Lake and tributaries.

Benson Drucker (1961–70)
- Coho salmon life history in the Karluk River system (1956, 1961–68).
- Detailed spawning study and survival of sockeye salmon of Grassy Point Creek.
- Subpopulation determination of sockeye salmon in Karluk Lake and its tributaries.
- Juvenile sockeye salmon age, size, abundance, and distribution in Karluk Lake (1961–63).
- Migratory behavior of sockeye salmon fry and smolts in Karluk Lake and River.
- Bear predation on adult sockeye salmon in two Karluk Lake tributaries (Grassy Point and Halfway Creeks) (1966–68).
- Total outmigration of sockeye salmon smolts determined (1961–69).
- Spawning surveys of sockeye salmon in Karluk Lake and tributaries.

Fisheries Research Institute, University of Washington

William F. Thompson (1948–58)
- Research emphasized that many independent subpopulations were present in the sockeye salmon run (1950).
- Reported that the midseason sockeye salmon at the Karluk River were depleted by the commercial fishery, causing the bimodal seasonal distribution of the run (1950).
- Claimed that counting weir may harm sockeye adults and fry by restricting their free movements.
- Changes proposed in the management of Karluk River sockeye salmon.

Table 2-1 (cont.)
Historical outline of fisheries research in the Karluk River basin, 1880–1970.

Donald E. Bevan (1948–58)

- Ocean migrations of sockeye salmon along west coast of Kodiak Island determined by tagging study.
- Length-frequency data of adult sockeye salmon collected from the fishery and spawning grounds to show the existence of subpopulations (1948–58).
- Spawning surveys of sockeye salmon in Karluk Lake and tributaries (1948–55).
- Spawning surveys of pink salmon of the Karluk River (1950–83).
- Limnological sampling of Karluk Lake (1951–54).
- Karluk River discharge rating curve (1954).
- Karluk Lake weather data (1950–54).
- Historical data gathered on sockeye salmon catches and cannery case packs.
- Karluk River explored for a counting tower location to replace the weir (1955).
- Reviewed past research results and published paper on decline of Karluk sockeye salmon runs (with Richard Van Cleve).

Charles E. Walker (1950–55)

- Juvenile sockeye salmon studies in Karluk Lake, River, and tributary streams (1950–55).
- Smolt age, size, run timing, and index of abundance in Karluk River (1954).
- Limnological sampling of Karluk Lake.
- Explored Karluk River for a counting tower location to replace the weir (1955).
- Spawning surveys of sockeye salmon in Karluk Lake and tributaries (1950–1955).

Richard Van Cleve

- Past research results reviewed and paper published on the decline of the Karluk sockeye salmon runs (with Donald E. Bevan).

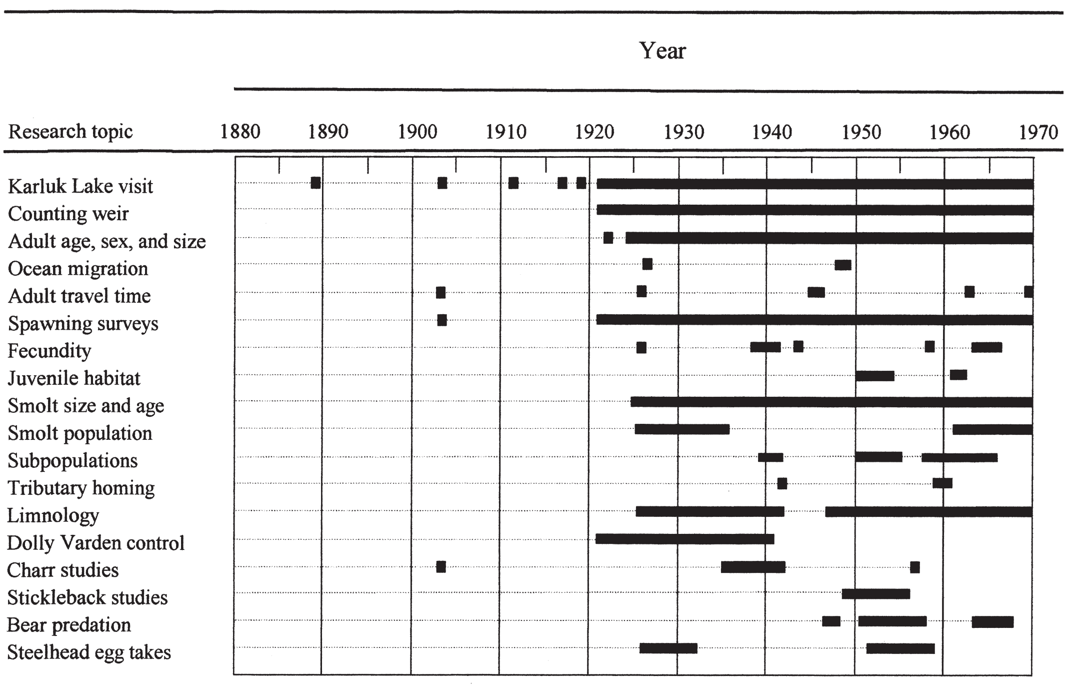


Figure 2-1. Summary of fisheries research at Karluk Lake and River, 1880–1970.

stopped its long-term research on Karluk's sockeye salmon, while the State of Alaska increasingly assumed research and management responsibilities for these fishery resources (Clark et al., 2006). This distinct change in governmental responsibilities gave a convenient endpoint for our historical discussion, though sockeye salmon studies at Karluk have continued to the present, and the recent era of biological research has produced numerous significant results, many being described in later chapters.

Tarleton H. Bean

1880

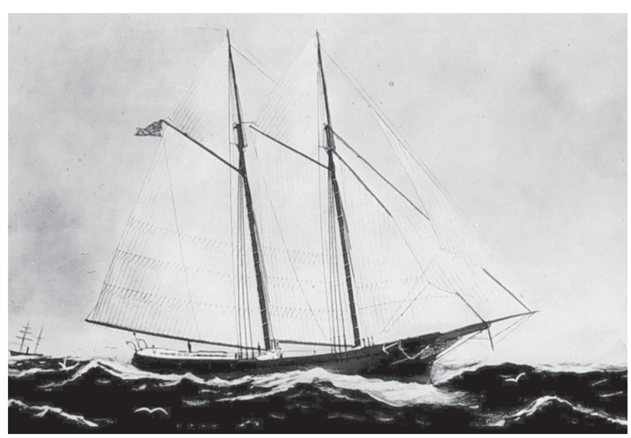
U.S. government involvement in Alaskan salmon research began in 1880 when the U.S. Census Bureau and the U.S. Commission of Fish and Fisheries (USFC) made plans to examine the fishery resources of its poorly known territories, which then included Alaska (Dunn, 1996; Pietsch and Dunn, 1997). Spencer Fullerton Baird, Commissioner of Fish and Fisheries, sent Tarleton

Tarleton Hoffman Bean (1846–1916). (Smithsonian Institution Archives, Record Unit 7177, George P. Merrill Collection, Negative #96-4529)

Hoffman Bean to Alaska in the summer of 1880 to investigate its fish and fisheries, and to collect biological specimens for the U.S. National Museum. Bean, then curator in the Division of Fishes and editor of the Proceedings of the U.S. National Museum, Washington, DC, was well qualified for the assignment. Although he earned an M.D. degree in 1876 from Columbian College, his real passion was the scientific study of fishes, and this was the career he pursued for his entire life.[2] He had first joined the Division of Fishes as an assistant ichthyologist in 1877.

Bean departed San Francisco on 13 May 1880 aboard the U.S. Coast Survey schooner *Yukon*, commanded by William Healey Dall, and for the next six months (May–October) traveled along the Alaska coast, exploring as far north as the Arctic Ocean.[3] On the outward voyage, they briefly stopped at Kodiak on 9–14 July and collected fishes in the immediate vicinity. Apparently Bean did not visit the Karluk River in 1880, but he learned of the river and its salmon resources and fishery by talking with several Kodiak residents: William J. Fisher, a U.S. Coast Survey tidal observer; Benjamin G. McIntyre, an agent of the Alaska Commercial Company; and two men involved in salting and drying Karluk River salmon, Captain H. R. Bowen of the Western Fur and Trading Company and Charles Hirsch of the Smith and Hirsch Company.

From the 1880 interviews at Kodiak and later correspondence, Bean learned that five species of Pacific salmon and Dolly Varden returned to the Karluk River each year. In 1880 Russian names were still used for these fishes, including “krasnoi riba” (sockeye salmon), “keezitch” (coho salmon), “chowichee” (Chinook salmon), “gorbuscha” (pink salmon), “hoikoh” (chum salmon), and “sumgah” (Dolly Varden). Bean learned that the Karluk River had a lagoon near the ocean and was fed by a large lake, reportedly 27 km upstream. Since two companies then salted and dried salmon at the river’s mouth, he obtained data on their annual harvests, number of employees, and facilities used in the fishery (Bean, 1887). Sockeye salmon, caught in a 46 m beach seine, were the main species being harvested and salted, though other salmon species were being dried. Bean clearly described the bimodal seasonal pattern of Karluk’s sockeye salmon runs, with the pink salmon run being interposed between the two sockeye peaks. The pink salmon run of 1880 was so large that he claimed it blocked other salmon species from entering the river. Once Bean learned that large salmon runs returned each year to the Karluk River, he realized this location had important fishery potential and stated that “there is perhaps no better place in Alaska for the establishment of a great salmon fishery” (Bean, 1887).



U.S. Coast and Geodetic Survey schooner *Yukon.* (National Oceanic and Atmospheric Administration Photo Library, NOAA Central Library, theb0372)

[2] Columbian College in Washington, DC is now known as George Washington University.

[3] Bean published part of his 1880 journal (11 August–17 September) that described the northernmost extent of the *Yukon* voyage to Alaska and Siberia (Bean, 1902). During the 1880 voyage, Bean collected 77 species of birds, 84 species of fish, and 110 species of lichen, some of them new to science.

Typical of naturalists from that period, Bean returned to Washington, DC, from Alaska with many specimens of plants, birds, and fishes for the U.S. National Museum collection. These travels and collections formed the basis for his later publications in the Proceedings of the U.S. National Museum and the popular magazine *Forest and Stream* (Bean, 1882, 1887, 1889).

In August 1881, Lucien M. Turner of the U.S. Army Signal Service briefly stopped at Karluk and observed its fishes, birds, and commercial fishing activities (Turner, 1886). Two companies then harvested its sockeye salmon and Dolly Varden, packing these fish into barrels with salt for eventual sale in San Francisco markets; over 3,000 barrels were prepared that year. He reported that 30–50 sharks (apparently, the spiny dogfish, *Squalus acanthias*) had gathered at the Karluk River mouth in mid-July to prey on the returning salmon and that village residents harpooned some of these large predatory fishes, which were prized for their liver oil.

1889

Bean's prediction of Karluk's great fishery potential was soon realized, starting in 1882 when Oliver Smith and Charles Hirsch built the first cannery on Karluk Spit. The cannery, eventually named the Karluk Packing Company, operated without competition for six years (1882–87), each year increasing its harvest and case pack production of sockeye salmon. Other entrepreneurs soon noticed the success of this commercial venture, and new canneries that took salmon from the Karluk River were built, four in 1888 and three more in 1889 (Fig. 2-2). Annual harvests of sockeye salmon rapidly grew from 1,000,000 fish in 1887, to more than 2,500,000 fish in 1888, and over 3,000,000 fish in 1889. To capture the 1888 salmon run, a wire fence was installed across the lower Karluk River, forming a complete barrier to upstream migration and concentrating the fish for easy capture.

News of the migration barrier and huge salmon harvests at Karluk soon reached federal authorities in Washington, DC. In January 1889 Marshall McDonald, U.S. Fish Commissioner, expressed concern about the sustainability of Alaska's salmon if river barricades were allowed and harvests increased even more. He presented his information about Alaska's fisheries to Poindexter Dunn, Chairman, House Committee on Fisheries, 50th Congress, and urgently recommended legislation to protect these fishery resources:

> [Karluk River salmon fisheries, 28 January 1889] This past season parties on the Karluk River, on Kodiak Island, conceived the idea of putting up a tight dam, merely using stakes and wire netting, intending no doubt to take what fish they required and allow the remainder to pass up to the lake, but no less than four other canneries started for the same place; consequently, to supply all, the river was closed from in May to October, the fish surging back and forward with the tide. The result was one company packed over 100,000 cases of salmon, and all the rest filled all their cans and made a perfect success. No care was taken of the surplus fish, and tens of thousands rotted on the banks . . . I beg to suggest to your honorable committee that prompt measures are necessary upon the part of the Government to place the salmon fisheries of the Alaskan region under such conditions as will insure their permanence. To prevent the ascent of the salmon to their spawning grounds will certainly result in a few years in the destruction of this valuable fishery. The erection of dams or barricades across the rivers, and the use of fixed contrivances for the capture of salmon in the rivers should be prohibited by law, under sufficient penalties actively and stringently enforced. (McDonald, 1889)

Congress responded on 2 March 1889, outlawing the use of river barriers to block salmon migrations and giving the Commissioner authority to investigate the conditions of Alaska's salmon and the methods used in the fisheries (Bean, 1891). Information gained from any inquiries would then be used to enact additional fisheries regulations.

McDonald sent Bean to Alaska in the summer of 1889 to begin the salmon investigations. At that time, Bean served several professional roles in Washington, DC, including ichthyologist for the USFC, editor of reports and bulletins for the commission, and curator in the Division of Fishes, U.S. National Museum. After his previous trip to Alaska, he had earned his M.S. degree at Indiana University in 1883 while studying under David Starr Jordan (Jennings, 1997). Bean was selected for the Alaska studies because of his familiarity with the region gained in 1880 and for his fisheries expertise. McDonald instructed him to start the investigations on Kodiak Island and, if time permitted, to examine the salmon fisheries at Afognak Island, Bristol Bay, and Cook Inlet (Bean, 1891).

Bean departed Washington, DC, in mid-June and proceeded to Karluk with his assistant Robert E. Lewis, surveyor Franklin Booth, and fish culturist Livingston Stone. They reached Karluk on 2 August, well into the field season and after early-run sockeye had already ascended the river. They established headquarters in the Karluk Spit office of the Karluk Packing Company, and the cannery owners assisted their inquiry by providing them transportation, supplies, and shelter. Because of the limited time and poor transportation to other can-

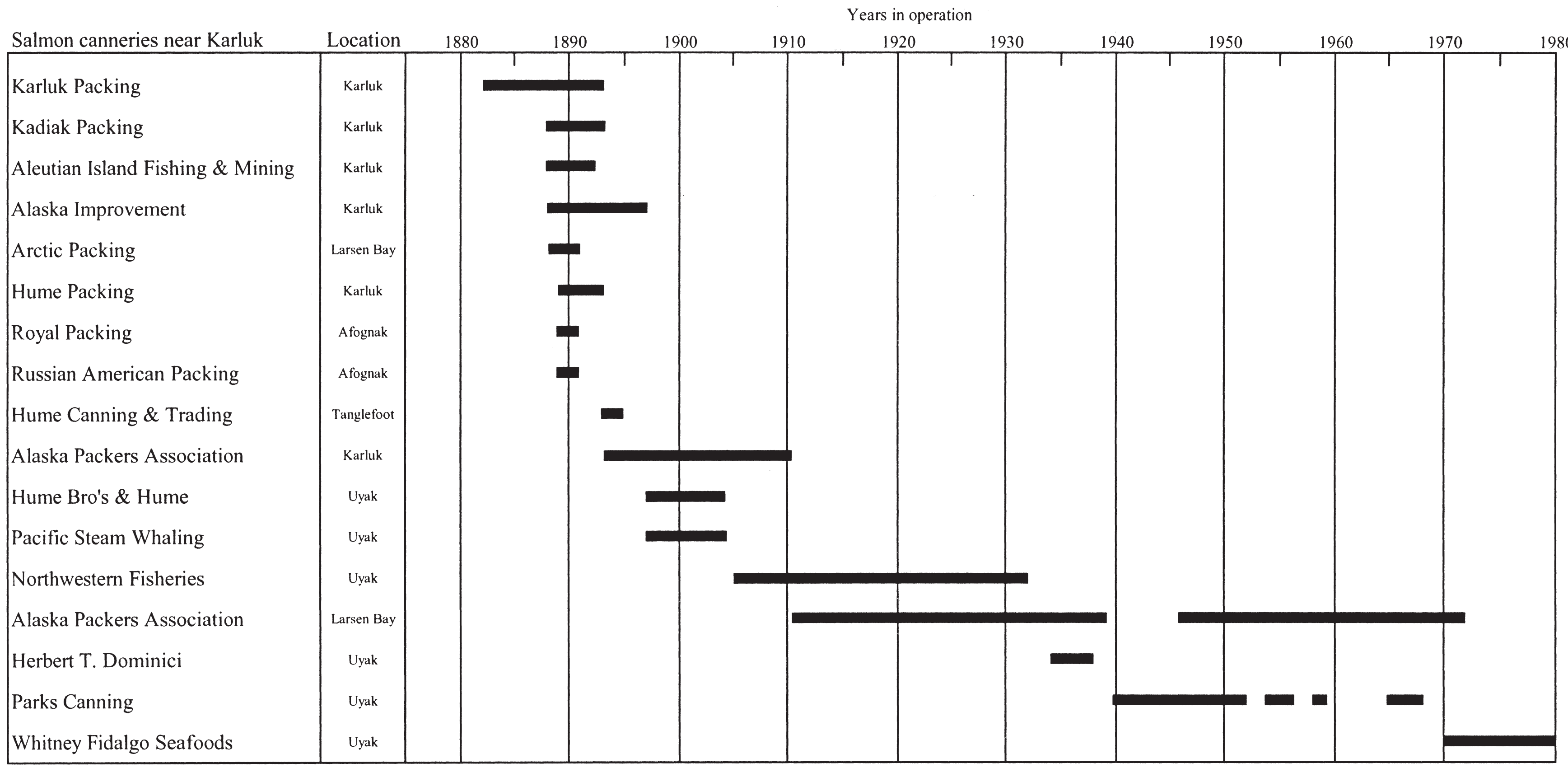
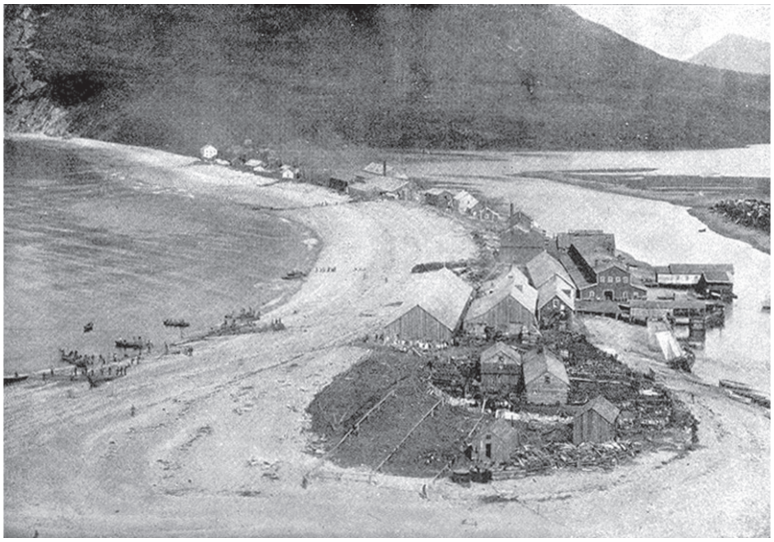


Figure 2-2. Summary of the salmon canneries that operated at or near Karluk, 1880–1980 (adapted from Roppel, 1986).



Karluk Spit salmon canneries (center), ocean beach seining (left), and Karluk River and Lagoon (right), 1889. (Tarleton H. Bean, from Bean, 1891)

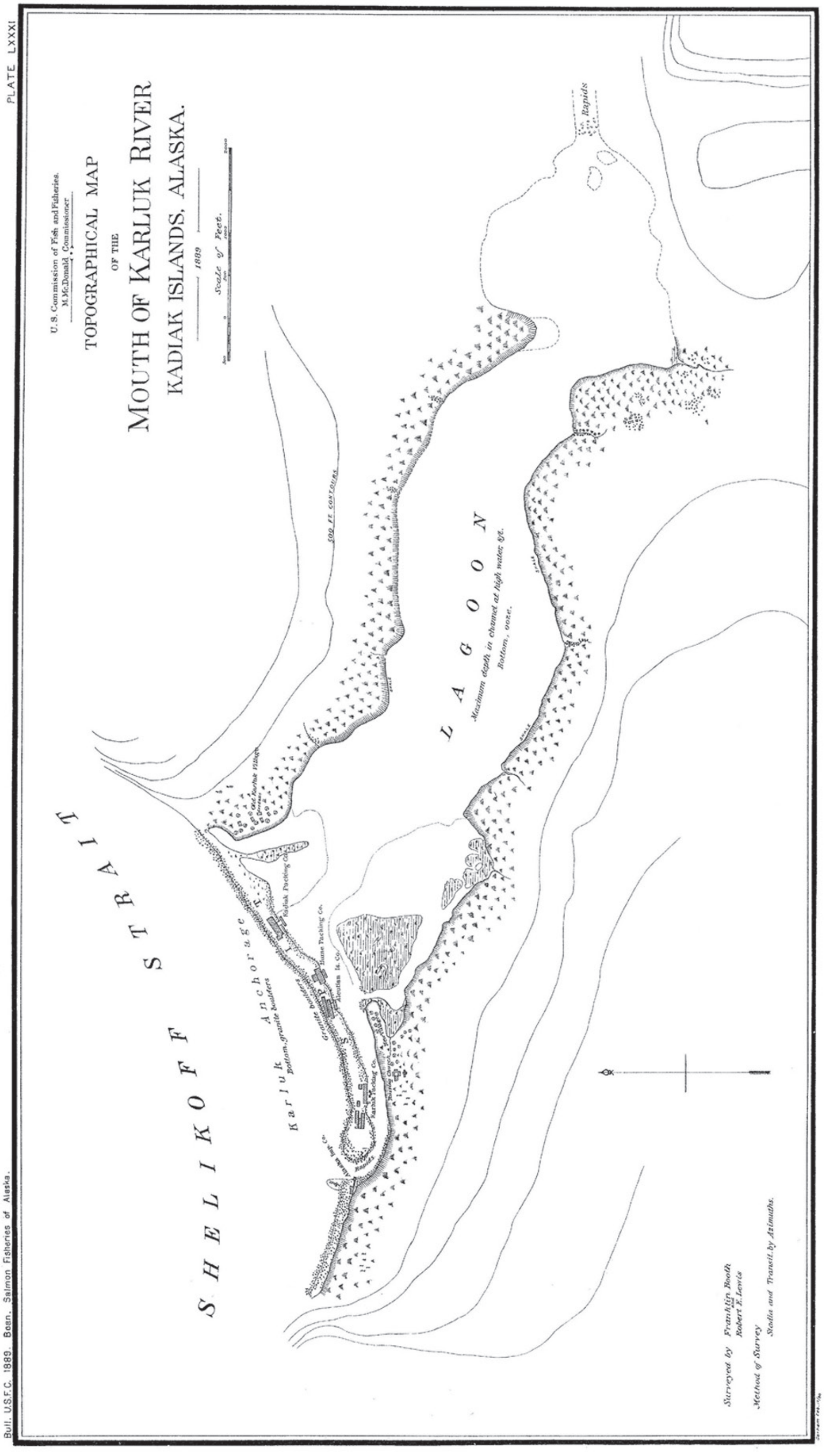
neries in the region, Bean focused his entire effort in 1889 on Karluk's salmon and fisheries, feeling justified in this decision because the Karluk River then supplied about half of Alaska's total salmon harvest. He stayed at Karluk for one month, departing 7 September for the return voyage to San Francisco. Despite this rather brief inquiry, he wrote the first detailed and published description of the Karluk River system, its salmon resources, and the fishery operations (Bean, 1891). His study marked the beginning of a long and concentrated effort to understand the biology of Karluk River sockeye salmon.

From his 1889 visit to Karluk, Bean described the region's physical geography, rugged coastline along Shelikof Strait, Karluk Anchorage, Karluk Spit, and Karluk Lagoon. He gathered data on tides, water temperatures, shoreline substrates, and regional vegetation. His map of Karluk Lagoon and Spit showed the locations of five canneries, old and new Karluk Village, and the newly constructed Russian Orthodox Church. Although a detailed Russian drawing of Karluk Lagoon already existed in 1867[4], and cruder versions had been present for several decades, Bean's was the first widely published map.

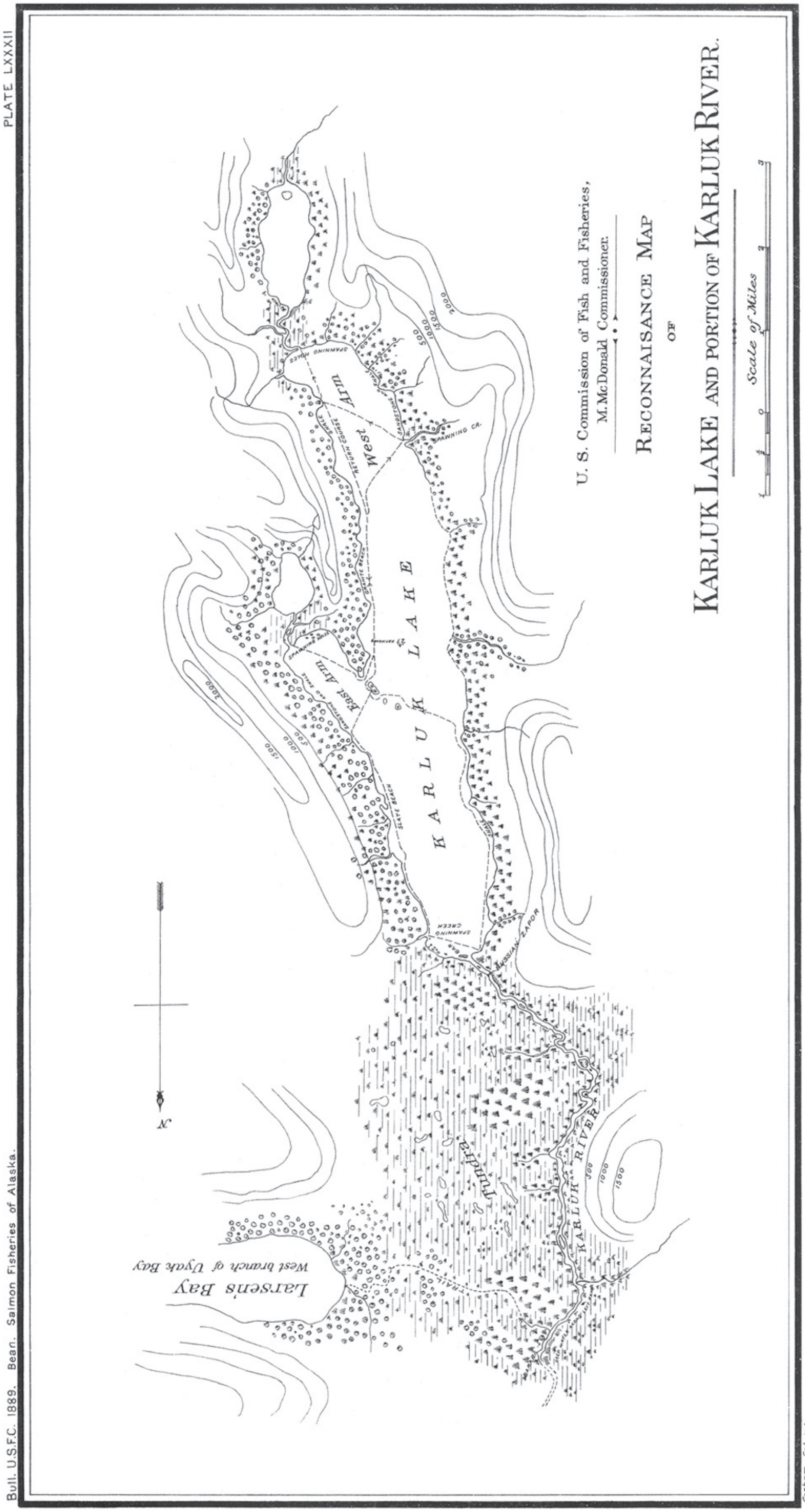
Likewise, he provided the first detailed map of Karluk Lake and the upper Karluk River between the Portage and lake, showing the location of many salmon spawning streams and lake beaches, tributary lakes, shoreline substrates, Portage barabara (native dwelling), and upper river zapor (weir-like salmon barrier). Considering his brief visit, these maps were reasonably accurate, being made with surveying instruments (theodolite transit, steel measuring tape, and aneroid barometer). Supplementing the descriptions and maps, Bean took many photographs of the Karluk Spit, River, and Lake, these first views of the region becoming important historical records. He had prepared for this task by being specially instructed in the new photographic methods at the U.S. National Museum in 1888 or early 1889 (Smithsonian Institution, 1891).

Karluk Spit, the narrow 1 km long bar at the mouth of the Karluk River, was the center of commercial salmon fishing and cannery operations in 1889. Here, Bean found that sockeye salmon were the most abundant and valuable commercial fish packed by the canneries, with about 13 sockeye needed for each case of canned salmon (one case = 48 1-lb. [0.45 kg] cans); whole sockeye salmon weighed about 3.2–3.6 kg each. For this early fishery, he described the harvest methods of beach seine crews and the steps needed to process and can the salmon, in addition to recording data on seine size and location, numbers and types of vessels, values of canning facilities, and employee nationality and wages. Beach seines had increased in length from 46 m in 1880 to 270–460 m in 1889, capturing vast numbers of sockeye salmon. Because of the keen competition for salmon in 1889, fishermen had shifted some beach seine sites from Karluk Lagoon and River to the ocean side of Karluk Spit. On the lower river, Bean saw the remains of the wire fence that had blocked the upstream salmon migration in 1888 and early 1889, but he was unconcerned that this illegal barrier might be reinstalled after his departure because competing canneries closely watched their rivals for unlawful fishing. Yet it alarmed him that nonstop

[4] Davidson, George. 1867. Plan reki Karluka = River Karluk, west coast Kodiak. Unpubl. map. Located at Bancroft Library (G4372.K3 1867 P5 Case XD), University of California, Berkeley, CA.



Map of Karluk Lagoon, Spit, and Village, 1889. The map identifies five salmon canneries located on Karluk Spit or immediately adjacent. The Karluk River enters the east end of Karluk Lagoon, flows though the lagoon, and enters the ocean at the west end of Karluk Spit. (Surveyed by Franklin Booth and Robert K. Lewis, from Bean, 1891)



Map of Karluk Lake and upper Karluk River, 1889. The map shows Bean's travel route around the lake and a Russian zapor in the upper Karluk River. (From Bean, 1891)

Native semi-subterranean dwelling (barabara) and dried sockeye salmon (ukali), Karluk, 1889. (Tarleton H. Bean, National Oceanic and Atmospheric Administration Photo Library, fish7461, from National Archives, Washington, DC)

Beach seining in the ocean for sockeye salmon, Karluk Spit, 1889. (Tarleton H. Bean, from Bean, 1891)

Beach seine crew, Karluk, 1889. (Tarleton H. Bean, National Oceanic and Atmospheric Administration Photo Library, fish7459, from National Archives, Washington, DC)

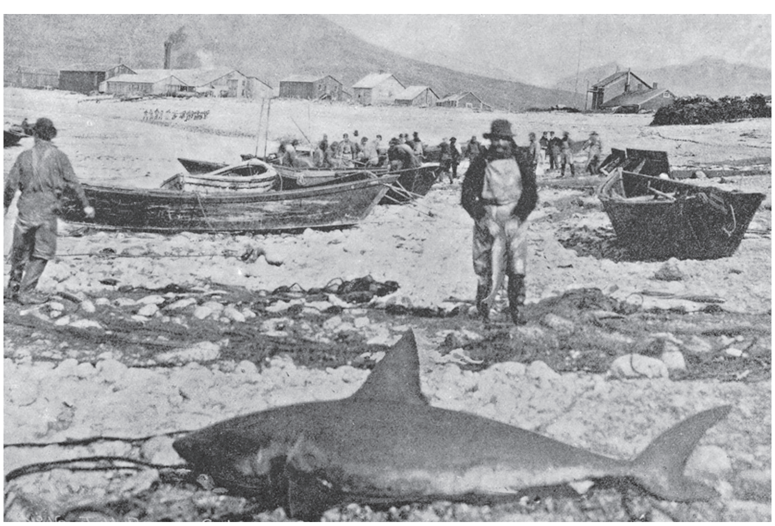
seining at the river's mouth would, in effect, bar salmon from entering the river and reaching the spawning grounds. He believed that the large and rapidly increasing harvests of sockeye salmon were unsustainable, and he warned that these runs would soon decline.

While at Karluk Spit, Bean observed the migratory behavior of sockeye salmon and interviewed experienced cannery personnel about the salmon runs. Little was then known about the ocean life of any Pacific salmon, and there was no appreciation that these fish had traveled long distances from the Gulf of Alaska before they arrived at the Karluk River. Instead, most people thought that the salmon traveled only short distances from local ocean sources. Bean saw that the bull kelp, *Nereocystis luetkeana,* off Karluk Spit served as a salmon refuge from the seines, and he watched the sockeye enter the river on flood tides, only to re-enter saltwater on ebb tides. Small sockeye (jacks or grilse), usually males, were infrequently seen in the migrating schools. Bean photographed a salmon shark, *Lamna ditropis,* that was caught in a beach seine and added this species to a growing list of salmon predators. He learned from cannery workers about the seasonal run timing of Karluk's other salmon species (Chinook, coho, pink, and chum), steelhead, and Dolly Varden, and that many young salmon descended the river each spring. From his own experience, and that of others, Bean rightly concluded that sockeye only ascended rivers draining from a lake. He reported that the size of sockeye salmon adults varied by season and location, though it is unclear if this was a general comment for all of Alaska or for only the Karluk run. If the latter, his early statement hints at the presence of subpopulations in Karluk's sockeye salmon.

Bean was the first biologist to visit and describe the sockeye salmon's spawning grounds at Karluk Lake. After watching masses of sockeye being caught in the beach seines at Karluk Spit, he was eager to see first-hand the productive source of these huge salmon runs at Karluk Lake:

> After we had seen the fishing gangs of the canneries landing their tens of thousands of red salmon almost daily, and one particularly favorable Sunday running the catch up to about 150,000, we were all the more anxious to see the spawning grounds of these struggling myriads. The river would be considered a rather small creek at home, yet it yielded as many red salmon this summer as all the other streams of Alaska combined. It was evident that some explanation of the annual occurrence of such immense shoals of fish would be found in the lake out of which the Karluk starts on its devious course, and we determined to reach Karluk Lake if possible.

Bean visited Karluk Lake on 15–22 August, along with his assistant Lewis, surveyor Booth, and fish culturist Stone. Proceeding upstream from Karluk Spit was impracticable because the river was too low and a hike along its banks was too difficult. Consequently, they traveled 54 km by ocean on a cannery vessel to the head of Larsen Bay, hiked 4 km on the trail to the Karluk River, and then proceeded 14 km upriver to the lake, arriving there on 17 August. Bean hired seven native guides from Karluk to assist the field party. For the next 4–5 days, they traveled around Karluk Lake in two 3-hatch bidarkas, observing sockeye salmon at spawning sites in the lake's small tributaries and scattered along the shore zone. Bean and Stone expected the spawning grounds to teem with adult sockeye, but few live fish were seen, causing them to infer that the commercial fishery had already taken most of the present run in the lower river. They also examined Karluk Lake as a possible hatchery site, but felt it was too inaccessible and, if used, would need a road from Larsen Bay.



Salmon shark captured in a beach seine, Karluk Spit, 1889. (Tarleton H. Bean, from Bean, 1891)

During their August travels around Karluk Lake, numerous sockeye carcasses littered the spawning grounds, indicating that many adult salmon had reached the lake in June and July. These observations—abundant sockeye spawners in June–July, followed by mid-August scarcity—were particularly significant since they indicated that a bimodal run distribution existed in 1889, with a slack period between the spring and fall peaks. The many carcasses provided Bean with dramatic evidence that all sockeye salmon died after spawning, a fact not yet fully accepted by fish biologists. Though he did not link the salmon carcasses to the lake's productivity, he was the first biologist to see these abundant remains and the organically-modified shoreline sediments.

Bean's observations at Karluk Lake included a wide variety of the region's flora and fauna besides sockeye salmon. While traveling up the Karluk River, he noted abundant aquatic plants growing in slower reaches. He found that juvenile salmon (40 mm length) were abundant in the lake's littoral and assumed that they had been produced by the previous year's spawning. Being a keen observer, he noted small parasites in and on the salmon and Dolly Varden. Salmon predators drew his attention, especially the sculpins and Dolly Varden, which ate many salmon eggs. He saw many sticklebacks in the lake and believed they also ate salmon eggs. Upon shooting several terns and gulls at the lake, he found that they had eaten young salmon. Bears were seen feeding on adult salmon and Dolly Varden (Bean, 1894):

> The enemies of the salmon are numerous. Small fish called sculpins, or miller's thumbs, swarm in the nests and eat large quantities of the eggs. Trout devour great numbers of eggs and young salmon. Gulls, terns, loons, and other birds gorge themselves with the tender fry. When the young approach the sea they must run a cruel gauntlet of flounders, sculpins, and trout; and in the ocean a larger and greedier horde confronts them. There the adults are attacked by sharks, seals, and sea lions. Before they have fairly entered the rivers huge nets are hauling them to the shore almost every minute of the day, during six days in a week. When they reach their spawning-grounds, bears are waiting to snatch them from the water and devour them alive. The salmon, it appears, would have been better off had it never been born in fresh-water, where its dangers are cumulative and deadly.

During the brief visit to Karluk Lake, Bean circumnavigated the entire lake and spent at least one night in the Camp Island barabara before proceeding down river on 21–22 August. Soon after returning to Karluk Spit, the 1889 field party departed on their return voyage south. Bean returned to Washington, DC, with specimens of Karluk's fishes, plants, and birds for the U.S. National Museum.

Viewed by present day standards of fisheries research, Bean's 1889 investigations at Karluk would be classed as a reconnaissance survey. He did not conduct detailed studies of sockeye salmon biology or life history, but he did make many natural history observations of sockeye and other fish species. Bean was the first biologist to visit and describe the sockeye's spawning grounds at Karluk Lake, and his biological observations continue to be relevant and of interest. He provided a unique view of the sockeye salmon runs as they existed in the early fishery, possibly before they were greatly modified by many more years of large harvests. Yet, it is prescient that Bean, the first biologist to study Karluk's sockeye salmon, predicted their coming decline in abundance. While many of his observations would now be considered to be well-known facts, he was the first biologist to investigate and publish them. At the time, these field observations gave new scientific information about Karluk's sockeye salmon. We are indebted to Bean for providing a clear and detailed view of conditions at the Karluk Spit canneries and Karluk Lake spawning grounds in 1889.

Cloudsley L. Rutter

1896–97

In the years following Bean's 1889 investigation, special agents of the U.S. Treasury Department made brief summer visits to Karluk's salmon canneries to collect statistics on the sockeye harvests and fishery

Cloudsley Louis Rutter (1867–1903). (G. S. Myers/A. E. Leviton Portrait File in the Natural Sciences, Archives, California Academy of Sciences, San Francisco, CA)

Karluk Lagoon (left), Karluk Spit canneries (center), ocean (right), viewed from east hill, Karluk, 1897. (Harry C. Fassett papers, Box 4 Book II, California Academy of Sciences Archives, San Francisco, CA)

Fish bins full of salmon at Hume Cannery, Karluk Spit, 1897. (Harry C. Fassett papers, Box 4 Book II, California Academy of Sciences Archives, San Francisco, CA)

Beach seining for sockeye salmon, Karluk Spit, 3 August 1897. U.S.S. *Albatross* anchored offshore. (Harry C. Fassett papers, Box 4 Book II, California Academy of Sciences Archives, San Francisco, CA)

Beach seining in the ocean for sockeye salmon, Karluk Spit, 1901. Photograph entitled "An 80,000 haul, Karluk, 1901." (Alaska State Library, Wickersham State Historical Sites Photograph Collection, P277-008-065)

Karluk village and River (near), Karluk Spit buildings (center), Shelikof Strait and ships (far), 27 September 1900. Photograph entitled "Ship *Indiana* leaving Karluk." (W. C. Fitchie, William J. Aspe Collection, Anchorage Museum, Gift of Mary Rolston, B1990.13.5)

Alaska Improvement Co. dock and cannery on west bank of Karluk River, Karluk, 1900–01. Karluk River at entry to ocean. (W. C. Fitchie, William J. Aspe Collection, Anchorage Museum, Gift of Mary Rolston, B1990.13.6)

operations. Apparently, the first such inspection occurred in 1892 (Pracht, 1898). Though these special agents only visited Karluk for 1–2 days each year, they tried to enforce the fisheries regulations, received complaints from rival cannery superintendents, and observed the canning and fishing activities. Since their enforcement areas in Alaska were extremely large and travel between canneries was difficult, these agents had no time for biological studies of salmon. Thus, little biological information was gained about Karluk's sockeye salmon and the spawning grounds during this period.

George R. Tingle (1897), U.S. Inspector of Salmon Fisheries, visited Karluk Lake on 15 August 1896 and found it "well stocked with red salmon." He noted the presence of the new APA hatchery on Karluk Lagoon, a modern facility of fish culture intended to boost sockeye salmon runs by incubating thousands of eggs and releasing fry back to the river. James A. Richardson was the hatchery's superintendent.

One employee at the Karluk Lagoon hatchery in 1896–97 was the young zoologist, Cloudsley Louis Rutter, who had just taken his Bachelor and Master of Arts degrees in zoology (1896) while studying under Charles Henry Gilbert at Stanford University, then renowned for its ichthyology and fisheries biology faculty (Brittan, 1997; Dunn, 1997).[5] In addition to his fish culture work at the hatchery, Rutter pursued wider scientific interests by collecting fishes, birds, mammals, and plants in the Karluk area; these specimens were eventually added to the Stanford University Museum (later transferred to the California Academy of Sciences), University of California Museum of Vertebrate Zoology, and U.S. National Museum (Seale, 1898; Grinnell, 1901; McGregor, 1901; Friedmann, 1935b; see also the Appendix). He collected and published information on the tide-pool fishes of Karluk (Rutter, 1899); this paper also contained data on two freshwater fishes, the coastrange sculpin, *Cottus aleuticus,* and threespine stickleback, *Gasterosteus aculeatus.* Beyond his work at the hatchery, there is little indication that Rutter did biological studies of Karluk's sockeye salmon in 1896–97, though he did travel to Karluk Lake and the upper river and saw the decayed salmon carcasses along the shorelines (Rutter, 1903a). Nevertheless, his fish culture work and time at Karluk prepared him for his later studies of its sockeye salmon.

1903

Between 1897 and 1902, special agents of the U.S. Treasury Department annually visited Karluk's canneries and hatchery to report on the salmon fisheries. Also in 1897 and 1900, Jefferson F. Moser, U.S. Navy Commander of the steamer *Albatross,* and several assistants visited Karluk to collect information on the salmon fisheries for the U.S. Fish Commission (Moser, 1899, 1902). On both visits, they focused on the commercial fishing and cannery operations at Karluk Spit (facilities, seine lengths and catches, case packs, employees, and vessels) and spent little time investigating sockeye salmon biology. During the 1897 visit, Alvin Burton Alexander, a fishery expert of the commission, spent a few weeks (18 July–6 Aug.) gathering fishery statistics and visiting the new hatchery at Karluk Lagoon. In the process, he learned from cannery personnel that adult sockeye salmon migrated to Karluk in two distinct runs, one in the spring of smaller fish and another in the fall of larger fish. As commonly happened, their 1897 visit coincided with the slack period between the spring and fall runs. Shortly after departing Karluk in 1897, Moser and Alexander unsuccessfully tried to reach Karluk Lake via Larsen Bay to view the spawning grounds. They claimed that few people, especially cannery personnel, had ever seen the spawning salmon at the lake. Surprisingly, they declared that Karluk Lake froze to the bottom in extreme winters and theorized that this event might explain the recent smaller runs of salmon. Their 1900 visit to Karluk lasted only three days (7–9 August), when Harry Clifford Fassett of the U.S. Fish Commission inspected the sockeye salmon hatchery and found it to be a model plant. His report focused on the hatchery facilities and operations, and he also gave some biological data on egg development times, fry predators, and the distinctness of the spring and fall runs. In 1900 the pink salmon run at Karluk was so large at its peak that beach seining for sockeye was temporarily halted.

By 1897–1900 it was well established in the scientific community that all salmon died after they spawned

[5] 1) Fisheries historian Mark R. Jennings, Davis, CA, personal commun. with Richard L. Bottorff, 1996.
2) One record of fish specimens in the U.S. National Museum (*Gymnelus*—USNM 00126717) indicates that Rutter visited Karluk in July 1894 and collected these fishes aboard the *Grampus.* Yet, the information on this museum record is difficult to interpret. We believe that the USFC schooner *Grampus* was primarily used along the east coast of North America and never sailed to Alaska. Possibly, these fish specimens were collected by another biologist and USFC vessel and mislabeled (or incorrectly dated). A second possibility is that Rutter was aboard the Pacific Steam Whaling Company steamer *Grampus,* which did operate in Alaskan waters during this period. The Pacific Steam Whaling Company did not have a salmon cannery near Karluk until 1897 (at Uyak).

and that adult sockeye only ascended rivers with headwater lakes, but it was still controversial whether or not adult sockeye salmon returned to their birth stream to spawn (the home-stream theory). This controversy continued even though fishermen around Kodiak Island already recognized unique characters in the sockeye they caught from different river systems. Sockeye salmon catches remained high during this period, but, even so, it was feared that the fishery was declining and that future large harvests were unsustainable because of overfishing. Seine hauls at Karluk Spit often captured 25,000–30,000 sockeye salmon at the peak of the run, while in previous years 100,000 fish were reportedly taken in a single haul (Moser, 1899; Rutter, 1903c). Moser expressed concern for the salmon's future and recommended new regulations and stronger enforcement of the commercial fishery. To manage this bountiful fishery, much greater scientific information was needed about its sockeye salmon.

In November 1902 President Theodore Roosevelt directed George M. Bowers, U.S. Fish Commissioner, to establish the Alaska Salmon Commission to study the condition of these fisheries (Roosevelt, 1904). Headed by David Starr Jordan and Barton Warren Evermann, this special commission included 12 other members selected mainly from the U.S. Fish Commission and Stanford University for their fisheries expertise (Jordan and Evermann, 1904). To do the salmon studies, members were stationed in 1903 at the most important salmon fisheries along Alaska's coast, from Southeastern Alaska to Bristol Bay. Cloudsley Rutter, a USFC employee since 1897 (U.S. Government Printing Office, 1897), and his assistant Milo H. Spaulding were chosen to study Karluk's sockeye salmon.[6] At the time, Rutter was one of the most knowledgeable Pacific salmon biologists, having earned this distinction for his recently completed landmark study of Sacramento River Chinook salmon in California (Rutter, 1903a).

Rutter and Spaulding spent about four months studying sockeye salmon at Karluk in 1903, from early May to late August or early September (Chamberlain, 1907). They maintained two bases of operations that summer, one at Karluk Spit and Lagoon by Rutter, and another at the north end of Karluk Lake by Spaulding, but with regular visits by Rutter.[7] From these two locations, they studied the adult sockeye salmon from the time when these fish first entered the river from the ocean until they reached their spawning sites at Karluk Lake. Similarly, they gathered data on the sizes, foods, and migrations of juvenile sockeye.

Although their 1903 field work was the first sustained biological study of Karluk's sockeye salmon, Rutter never directly published this information. Shortly after returning to California from Alaska, Rutter died on 29 November 1903 before completing a full report of the Karluk field work (Van Arsdale and Gerber, 1904; Jennings, 1987). Instead, many of his Karluk results were included in the 1907 paper by Frederic M. Chamberlain, another member of the Alaska Salmon Commission stationed in southeastern Alaska (Jennings, 1987). Chamberlain extracted and summarized data about Karluk's sockeye from the field notes and fish collections of Rutter and Spaulding.

Rutter's 1903 field studies at Karluk were extraordinary in that they focused on sockeye salmon biology,

Frederic Morton Chamberlain (1867–1921). (From Jennings 1987, courtesy of *Fisheries,* American Fisheries Society)

[6] By 1903 Rutter held the position of naturalist on the USFC steamer *Albatross* (Jordan and Evermann, 1904).

[7] 1) Fisheries historian Mark R. Jennings, Davis, CA, personal commun. with Richard L. Bottorff, 1996.
2) Letter (19 July 1903) from Spaulding, Karluk Lake, to Rutter [at Karluk Spit]. Located in Box 130, Barton Warren Evermann papers, Library Special Collections, California Academy of Sciences, San Francisco, CA.
3) Rutter, Cloudsley L. 1903. Memo notebook for 1903 (16 June–14 July), Karluk Spit, Portage, River, and Lake. Located in Box 130, Barton Warren Evermann papers, Library Special Collections, California Academy of Sciences, San Francisco, CA.

while all previous efforts had centered on the commercial fishing and cannery operations. At the time, many basic biological facts about sockeye salmon remained unknown, such as: 1) multi-year rearing of juveniles in a freshwater lake, 2) planktonic food habits of juvenile salmon, 3) multi-year aged smolts that migrate downstream each spring to the ocean, 4) ocean residence in the Gulf of Alaska and Bering Sea far from the Karluk River, 5) many combinations of freshwater and ocean ages of returning adult salmon (ages not yet determined by scale analysis), 6) fidelity of adults in returning to their home stream, and 7) uniqueness of the sockeye's life history from that of other salmon species. Rutter's investigations included scientific collections, natural history observations, and, for the first time, field experiments designed to answer specific biological questions. Significantly, since his study lasted four months and included most of the sockeye's spawning period, he observed the seasonal changes in this dynamic river-lake ecosystem.

Shortly after Rutter and Spaulding reached the Karluk region in 1903, they began their sockeye salmon studies at the lake. By late May they had installed a fish trap at the outlet to capture adult sockeye moving upstream (Chamberlain, 1907). To measure the sockeye smolt migration from Karluk Lake, they made five overnight sets of a fyke net at the outlet on 5–30 June, but it is unclear what was caught because Chamberlain reported that "salmon parr" and "salmon fry" were trapped, without identifying the species or giving their size. Chamberlain defined "parr" as being juveniles of any size so long as they had parr marks, while Rutter used this same term for young salmon of 100–200 mm length (Rutter. 1903c).[8] Using Rutter's definition, the fyke nets likely caught about 200 sockeye smolts in June. At Karluk Spit, Rutter collected many large juvenile sockeye that had been incidentally brought ashore in the commercial beach seines in June and July, though it is unclear if he realized that these were the recent smolt migrants from Karluk Lake (Chamberlain, 1907). Often as many as 1,000 salmon smolts, most likely sockeye, were caught in each beach seine early in the fishing season. Chamberlain (1907) remarked that Karluk's sockeye smolts were much larger than those produced in other lake systems of Alaska and Canada, but the reasons for this size difference were unknown.

In 1903 it was difficult for biologists to identify the young stages of all salmon species. To remedy this problem, Rutter preserved juvenile fish of many sizes and all species from a wide range of habitats: freshwaters of the lake, its tributary creeks, and river; estuarine waters of Karluk Lagoon; and the ocean at Karluk Spit. Further, he photographed and fully described the colors and marks of living specimens of all species.[9] Chamberlain later used Rutter's specimens and field notes to illustrate and taxonomically separate these juvenile salmon. At least some of Rutter's preserved sockeye specimens were also examined for their food habits; the young had fed on crustaceans and insect larvae in the lake's tributaries and upper river (May–July) and on planktonic crustaceans in the ocean.

Typical of most fish biologists who visited Karluk Lake, Rutter and Spaulding examined the spawning habitats and behaviors of adult sockeye salmon. They found many spawning redds in the lake's lateral and terminal streams and along its lakeshore, but their observations went beyond general surveys. In addition, they described the areas and substrates of spawning sites, the development of secondary sexual characters in adult salmon, the adult behaviors in digging and defending the redds, the male–female spawning behavior, and the eventual decline, death, and decay of adults.

To measure the number of spawning sockeye and their egg production, Rutter selected Moraine Creek for intensive study.[10] Here, all dead sockeye were periodically counted, checked for spawning condition, and removed from 5 August to 5 September, a total of 21,756 carcasses closely divided between males and females (Chamberlain, 1907). About 80% of females had completely deposited their eggs and 20% retained 100 eggs on average. By digging into spawning redds and using spawning baskets,[11] they concluded that

[8] Rutter, Cloudsley Louis. 1903. Field observations by Cloudsley Rutter on his Karluk work of 1903. Unpubl. notes. 48 p. Copy provided courtesy of Mark R. Jennings (Davis, CA) and located in Box 130, Barton Warren Evermann papers, Library Special Collections, California Academy of Sciences, San Francisco, CA.

[9] See footnote 7 (3).

[10] Rutter and Spaulding identified Karluk Lake's tributaries by number, not name; Moraine Creek was first formally named in 1921 by Charles H. Gilbert. The creek they intensively studied, apparently Moraine Creek, was identified as the second stream from the outlet on the east side of Karluk Lake. Most of Rutter and Spaulding's salmon spawning studies were confined to the northern end of the lake in the vicinity of Spring, Moraine, and Cottonwood creeks.

[11] A 1906 APA map shows the 1903 locations of Rutter's spawning baskets. APA 1906 reconnaissance map located at Alaska State Library, Historical Collection, Juneau, AK, and a copy at NARA, Anchorage, AK.

eggs buried deep in the gravel remained in good condition. From the number of females counted and an assumed fecundity of 3,500 eggs per female, Rutter estimated that the Karluk system produced 400,000,000 sockeye salmon eggs in 1903.

Rutter and Spaulding were the first biologists to study the migration speed and behavior of adult sockeye at Karluk. They tagged 400 spring-run sockeye and released them off Karluk Spit, finding that most entered the river within a day and few remained after a week. Rutter next attached copper jaw tags to hundreds of adult sockeye in Karluk Lagoon in June and released them for Spaulding to record their arrival at the lake, finding that they needed about 10 days to ascend the river (Chamberlain, 1907). A few tagged sockeye were later recovered off Karluk Spit, showing that some fish returned to the ocean after entering Karluk Lagoon. One tagged fish was recovered near the mouth of the Ayakulik River, over 60 km from Karluk, suggesting that sockeye salmon might ascend two different streams, a possible refutation of the home-stream theory (Jordan, 1903; Kutchin, 1904; Chamberlain, 1907).[12] While doing this tagging work, Rutter observed many details of the migratory behavior of adult salmon, including how they reacted to tides, winds, and river currents.

After completing the tagging work on the lower river in late June, Rutter and Spaulding next tagged 255 adult sockeye as they entered Karluk Lake on 3–25 July (Chamberlain, 1907). Most tagged fish were later recovered on the spawning grounds, but unexpectedly three were caught in seines at Karluk Spit, indicating that a few adult sockeye had descended the entire river and re-entered the ocean. Their tagging work at Karluk Lake, plus observations at the spawning streams, showed that adult sockeye had a 1-month maturation period between their June–July arrival at the lake and July–August spawning. Thus, Rutter and Spaulding obtained a remarkably accurate understanding of the entire upstream migration of adult sockeye between ocean, lagoon, river, lake, and specific spawning sites.

Based on his 1896–97 hatchery work and 1903 studies, Rutter declared that adult sockeye salmon returned to Karluk in two distinct and intergrading runs, the first peaking in late June and the second peaking in early August (Chamberlain, 1907).[13] The spring run was abundant in 1903 and Rutter stated that "apparently there was a considerable run of salmon during June, for there was certainly an enormous number reached the lake."[14] In fact, he estimated that "at least two millions reached the lake," a surprising number since this horde of salmon had passed by the Karluk Spit canneries unnoticed, the strong northeast winds keeping fishermen from setting their nets. And yet, for some reason, he claimed that the 1903 sockeye run was rather poor, the two runs not being observed. Since Rutter departed Karluk in late August, he possibly missed seeing the fall sockeye run.

When at Karluk Spit, Rutter often watched the frenzied beach seining activities and frequently examined fish samples from the catch. The adult sockeye hauled ashore had only eaten small crustaceans and fishes, foods he considered appropriate for their fine gill rakers (Chamberlain, 1907). These simple ocean foods suggested to him that it would be unnecessary for sockeye to migrate far from the Karluk River to be adequately nourished. Further, while observing these adult sockeye, Rutter noticed that many had body scars, and he carefully examined 500 individuals for wounds received in the ocean.[15] Over 10% had suffered some damage, mostly posterior body injuries. On the gill covers and posterior bodies of five adult sockeye, he found the characteristic circular mark made by lamprey (Rutter, 1903a).

Although Rutter and Spaulding focused their 1903 field studies on sockeye salmon, much of the region's flora and fauna interested them. Whenever possible, they collected fishes, birds and their eggs, and plants to deposit in several museum collections, such as Stanford University and the U.S. National Museum (see Appendix). In 1903 Rutter added to his previous collections of tide-pool fishes and was fascinated by the mass migration of threespine sticklebacks into Karluk's tributary lakes.[16]

Whenever at Karluk Lake, he kept notes on its numerous bald eagles, *Haliaeetus leucocephalus*, and often examined their nests for eggs and eaglets. Fifteen pairs of bald eagles nested at the lake in 1903 (Rutter, 1903b). Rutter and Spaulding also collected 230 plant specimens in the Karluk region (Hulten, 1940), but found it difficult to dry the pressed samples in the

[12] See footnote 8.
[13] See footnote 8.

[14] See footnote 8.
[15] See footnote 8.
[16] Rutter, Cloudsley Louis. 1903. Notes made by Mr. Cloudsley Rutter at Karluk, season of 1903. Unpubl. notes. 7 p. Copy provided courtesy of Mark R. Jennings (Davis, CA) and located in Box 130, Barton Warren Evermann papers, Library Special Collections, California Academy of Sciences, San Francisco, CA.

damp rustic conditions of the lake field camp.[17] To further document the region's biota, Rutter photographed its fishes and plants.[18] Beyond these wide-ranging biological interests, Rutter wanted to prepare an accurate map of the Karluk region and took compass bearings of prominent landmarks from good vantage points during his travels.[19] In 1903, during Rutter's time at Karluk, the U.S. Bureau of Fisheries (USBF) was created within the Department of Commerce and Labor.

Rutter's 1903 field observations provide many interesting insights into then prevailing ideas about the life history of sockeye salmon.[20] For example, where did sockeye salmon spend their ocean residence, close to the Karluk River mouth or far away? When salmon returned to the Karluk River, did they home to that specific river as a distinct stock or did they only return to it because it just happened to be the closest river? No one could unequivocally answer these questions in 1903.

There had been reports of salmon being washed aboard vessels in the mid North Pacific Ocean, hinting of a distant marine residence, but Rutter believed that the salmon remained fairly close to their spawning streams (Rutter, 1903c). He felt that long distance migrations were unnecessary since ample foods were readily available locally. Thus, he concluded that salmon did not home to a specific river, but only returned because it was the first river that attracted them. He believed that the salmon of Shelikof Strait, Chignik, and Cook Inlet had a common feeding ground where they intermixed, forming a common pool from which future runs were drawn, but not as distinct stocks returning to specific home streams. This theory seemed to explain why the millions of sockeye fry that had been released from Karluk's hatchery had provided few benefits to its runs; that is, the hatchery output was being absorbed by other regions.

By 1903, after 20 years of commercial fishing at different sites around Kodiak Island and Shelikof Strait, it was obvious that the size of adult sockeye varied between locations and that the Karluk River fish were smaller than at some other sites. Rutter believed that the ocean food supply of juveniles explained these size variations. He reasoned that juveniles spent their first ocean year near the mouth of their natal river and that their growth depended upon the habitat's food abundance. Furthermore, he thought the abundance and variety of juvenile foods were directly proportional to the size of the ocean bay at the river's mouth. In other words, rivers discharging into large ocean bays would have abundant food and rapid juvenile growth, while rivers discharging into small bays would have sparse food and slow juvenile growth. Thus, larger adult sockeye would be expected at Uganik and Chignik with large bays, while smaller fish would occur at Karluk and Little River with little or no ocean bays.

The large diversity of age compositions in Karluk's sockeye salmon runs remained unknown in 1903 because scale-aging methods had yet to be used on Pacific salmon. Biologists then had little idea that returning sockeye adults had many combinations of freshwater and ocean ages. When Rutter examined the sockeye catch statistics for Karluk, he noticed a 5-year cycle between good catches and concluded that adults were five years old, but he believed that the only accurate way to measure salmon ages was to mark juveniles and observe the later return of marked adults. This method was tried on several thousand sockeye fry released from Karluk's hatchery in 1897 and 1902, but the results were unclear because few marked adults were ever recovered (Chamberlain, 1907; Roppel, 1982).

Biologists realized by 1903 that most sockeye salmon returned to spawn in river systems having lakes, but the reason for this behavior was unknown. Rutter speculated that adult fish used the lakes while their reproductive products matured before spawning (Rutter, 1903c). He rightly contrasted the dramatically different salmon runs of the Karluk and Sturgeon rivers, these two adjacent watersheds discharging into Shelikof Strait only 8 km apart.[21] The Sturgeon River lacked a headwater lake and sockeye salmon, while the Karluk River flowed from a large lake and had a huge sockeye run. But how did returning adult sockeye recognize which rivers had lakes?

Rutter theorized they might be attracted to a lake-bearing river by seeing or smelling the juveniles present in the river or clustered around its mouth. Or possibly, returning adults could smell the adult carcasses that remained from the previous year's spawning. Clearly, he failed to understand the lake's importance as a multi-year nursery for juvenile sockeye; instead, he believed that once the egg-sac had been absorbed and fry could swim, they started on a slow migration downriver to the ocean. Thus, he claimed that juveniles spent little time in Karluk Lake and reported seeing few along its shores in 1903. Holding such views, he had no reason to collect limnological data at Karluk Lake. Never-

[17] See footnote 7 (2).
[18] See footnote 7 (2) and footnote 7 (3).
[19] See footnote 7 (3).
[20] See footnote 8.
[21] See footnote 8.

theless, only a short time later, Chamberlain (1907) began to reveal the unique life history of sockeye salmon and document that most juveniles reared for at least one year in a lake before they entered the ocean.

When Bean visited Karluk Lake in 1889, the idea that Pacific salmon died after spawning was just gaining acceptance among biologists, but by 1903 it was a known fact. Rutter discussed reasons for this phenomenon and realized that death after spawning was determined by a long evolutionary process on the salmon's life cycle.[22]

Rutter was the first Karluk biologist to examine the food habits of hundreds of charr collected from the lake, lagoon, and ocean. He wanted to test the widespread belief that charr intensely preyed on salmon eggs and young. No distinction was made in 1903 between the two charr species present at Karluk. Rutter referred to these fishes as "Dolly Varden trout,"[23] while Chamberlain called them charr. Despite examining many stomach samples, Rutter found little evidence of charr predation on sockeye fry, except at the unnatural habitat inside hatchery corrals. Though schools of salmon fry inhabited the upper river in June–July, charr stomachs lacked young salmon (Chamberlain, 1907). Nevertheless, charr ate many sockeye eggs and these were found in more than 50% of the charr examined from a creek with spawning sockeye.

Although the main purpose of the Alaska Salmon Commission was the biological study of Pacific salmon, members were also asked to evaluate the potential of hatcheries to enhance salmon production. Rutter outlined several advantages of locating a hatchery at Moraine Creek, a Karluk Lake tributary, including 1) an abundant supply of adult sockeye that could not be completely blocked by commercial fishing, 2) ripening ponds would be unnecessary for holding brood stock, 3) catching spawners would be easy, 4) a good water supply existed, 5) a good building site existed, and 6) Karluk Lake had almost no Dolly Varden to prey on sockeye fry.[24] His claim that few charr occurred at the lake was unusual; most biologists, before and after, reported them to be common. The main disadvantage of a Karluk Lake hatchery was the site's inaccessibility, which would require that a railway be constructed from Larsen Bay. Rutter criticized the low efficiency of the Karluk Lagoon hatchery, stating that many adult sockeye held in ripening ponds died before spawning. He concluded that "I think this hatchery has been of very little value."

In summary, Rutter's 1903 investigations at Karluk comprised a wide range of biological topics on sockeye salmon and the region's biota. Atypical for biologists of this era, his methods went beyond natural history observations, descriptions, and museum collections, and included for the first time field experiments to answer specific biological questions. Considering the relatively short field season spent at Karluk, the rustic living conditions, poor transportation, and limited field assistance, the scope of his studies and scientific accomplishments were remarkable. Rutter revealed many life history aspects of Karluk's sockeye salmon and his findings remain pertinent today. It is noteworthy that many of the topics he studied and methods he used fall within the discipline of fishery biology, which was then in its infancy. It is unfortunate that the full details of his pioneering research at Karluk were curtailed by his untimely death.

Following Rutter's 1903 studies, no further comprehensive investigations were done on Karluk's sockeye salmon for 15 years. Although sockeye salmon harvests were declining during these years, the yields still remained relatively high and apparently there was little urgency within the government or canneries to obtain basic biological data on this species. The APA discounted the need for a federal biological station in Alaska devoted to the scientific study of its salmon, but they did want the government to study fish processing technology:

> I do not think that the canners believe particularly that we should have a biological station, which I suppose would be perfectly proper for the fisheries to utilize. We do not care particularly about knowing how many scales there are to the square inch or whether the lateral line runs up or down or how big the peduncle is, or anything of that kind, but we do want to know how to utilize our products. (U.S. Senate, 1912)

Several USBF biologists briefly visited Karluk after 1903, most often to evaluate the operations and effectiveness of the sockeye salmon hatchery located on the lagoon. The APA first built this hatchery in 1896 as a private volunteer effort to help augment the runs at Karluk, but shortly thereafter this facility let them satisfy the 1900 and 1902 federal mandates that canneries must release 4–10 fry for every adult salmon caught. This requirement became less onerous in 1906 when the federal government began to rebate case pack taxes to those canneries that operated a hatchery (40 cent rebate for every 1,000 fry released).

[22] See footnote 8.
[23] See footnote 8.
[24] See footnote 8.

Despite the notable efforts of the APA to enhance the sockeye salmon runs at Karluk, the hatchery received increased criticism over the years because a large portion of the sockeye brood stock died before they spawned and the fry were released into the estuary, an unnatural rearing environment for these young fish. It was during this period (1903–07) that biologists first discovered that young sockeye reared for one or more years in a freshwater lake before they migrated to the ocean. This new fact immediately cast doubt on the hatchery practice of releasing fry into an estuary. To remedy the serious defects of the existing hatchery, the APA considered building a new facility at Karluk Lake or transporting the hatchery fry to the lake, but these ideas were never completed.

Fassett made a detailed inspection of the Karluk hatchery on 1–8 September 1910 and provided information on the spring and fall sockeye runs, egg size and fecundity, and fry biology.[25] Ward T. Bower of the USBF Division of Alaska Fisheries examined the hatchery in 1910 and 1911 (Bower, 1912). He explored Karluk Lake on 29 July–1 August 1911 to find a new hatchery site to replace the inefficient facility at Karluk Lagoon and noted huge numbers of sockeye salmon spawning in the lake's tributaries and in the shallow waters along its shorelines.[26] Chamberlain next inspected the hatchery in September 1911 and spoke favorably of its operations.[27]

When the U.S. Senate held hearings in 1912 on a bill (S 5856) to amend the laws that regulated Alaska's salmon fisheries and governed its federal taxation, the Karluk Lagoon hatchery came under intense scrutiny (U.S. Senate, 1912). Jefferson F. Moser, then an APA official, argued that the hatchery had benefited the sockeye returns at Chignik, a cannery located 160 km away on the Alaska Peninsula, but that Karluk's runs had not been helped. The consensus reached at the hearings by Moser, Bower, and Evermann (Chief, USBF Division of Alaska Fisheries) was that Karluk Lake would have been a much better hatchery site than Karluk Lagoon. It was also clear from the testimony that federal biologists and cannery officials did not know the ultimate fate of hatchery fry released into the lagoon, though various opinions were offered on their survivability. James Wickersham, Alaska's delegate to Congress, reported that an informant "had seen those little fish at the Karluk hatchery in windrows dead on the beach," but this evidence was discounted (U.S. Senate, 1912).

The U.S. Senate hearings of 1912 also focused attention on the APA commercial fishing and canning activities, which appeared to have few benefits for Alaskans. The use of fish traps by the large canneries had long angered Alaska residents because these ensnaring devices, erected each year at select locations along the state's coastline, appeared to give non-resident companies an exclusive fishing right (U.S. Senate, 1912). Moreover, in the pursuit of their commercial ventures, the early canneries bought few supplies and hired few employees from Alaska. Instead, they came to Alaska each spring on their own vessels that were already fully loaded with the necessary materials and laborers to harvest and process salmon for the full canning season. At the end of each season, they returned to San Francisco, Seattle, or other west coast ports with their laborers and salmon case pack, leaving a single watchman to guard the cannery buildings over the winter. Although

Alaska Packers Association ship *Star of Alaska,* ca. 1920. (Gabriel Moulin, National Park Service, San Francisco Maritime National Historical Park, San Francisco, CA, SAFR P80–084.1NL)

[25] Fassett, H. C. 1910. Report on the salmon hatchery operated by the Alaska Packers Association on Karluk Lagoon, Kadiak Island, Alaska. Unpubl. USBF Report. 25 p. Located at Alaska Historical Collections, Alaska State Library, Juneau, AK.

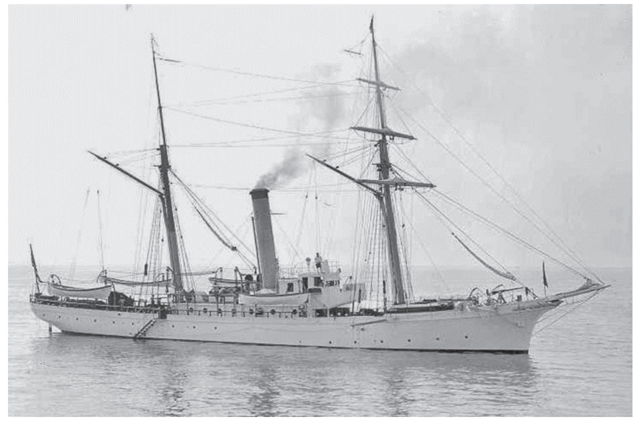
[26] 1) In 1910 he visited the hatchery on 7 May. Memo (7 October 1910) from Ward T. Bower, Department of Commerce and Labor, USBF, Washington, DC. Located at NARA, Anchorage, AK.
2) Apparently, Bower prepared a special report of his 1911 visit to Karluk Lake, but the details of this trip are unknown because the special report was not located. Letter (31 January 1927) from Ward T. Bower to Willis H. Rich, Stanford University, CA. Located at NARA, Anchorage, AK.
3) Bower related some of the information about his visits to Karluk Lake during his testimony at the Senate hearings of 1912 on Alaska's fisheries (U.S. Senate, 1912).

[27] Memo (16 April 1916) from Ward T. Bower, USBF, Washington, DC, to Commissioner of Fisheries, Washington, DC. Located at Alaska Historical Collections, Alaska State Library, Juneau, AK.

the canneries paid a tax on their case pack production (4 cents per case in the early years), little of this money went to improve Alaska's infrastructure, especially from companies that received tax rebates for operating a sockeye salmon hatchery. No other levies, including property taxes, were imposed on the early canneries in Alaska. All of these long-festering grievances were tersely voiced by Wickersham at the 1912 hearings, well before statehood, but anticipating that future change in governance (U.S. Senate, 1912).

Just prior to permanent closure of the Karluk Lagoon hatchery in 1916, USBF biologist E. M. Ball examined the facility in April and July and on the later date traveled upstream to the Karluk River Portage. Then, in 1917, Ball surveyed the spawning grounds at Karluk Lake on 12–14 September and saw sockeye salmon spawning in the upper Karluk River. He believed that artificial propagation of sockeye was unnecessary, declaring that "nature has made wonderful provision for the salmon of Karluk by supplying them with ideal spawning grounds and other favorable conditions." In fact, he wanted this productive system protected and suggested that "it would be a splendid thing to set apart by Presidential Proclamation Karluk Lake and its catchment basin as a National Fisheries Reservation in which salmon would be allowed to live out their lives in the reproduction of their kind . . ."[28]

Besides the biologists that briefly investigated the sockeye salmon, federal agents continued to visit Karluk for a few days each year during 1892–1915 to enforce the fisheries laws and gather information on the commercial fishing and cannery operations. But the task of monitoring and regulating the Karluk fishery was nearly impossible because these agents were spread across extensive enforcement areas and lacked suitable vessels for independent travel in the Kodiak region. Most agents did not live in Alaska near their enforcement areas, traveling to the region each summer from the coterminous United States. Their brief annual visits to Karluk were typically made on U.S. Treasury Department revenue cutters (*Grant, Perry, Rush,* and *Walcott*), and, at times, the



U.S. Revenue Cutter, *Commodore Perry,* Alaska service 1894–1910. (U.S. Coast Guard Historian's Office, Historic Image Gallery of Revenue Cutters)

agents depended on cannery vessels for transportation to the canneries inspected, completely removing the possibility of surprise visits. As a consequence, Karluk's salmon fishery in the early years was largely unregulated for most of the harvest season, and the enforcement agents relied on the honesty of the fishermen and canneries to abide by the laws. This resulted in many infractions of the fishery laws, but few violations were brought to the attention of the enforcement agents and, during this era, it was difficult to get convictions and significant penalties for fishing crimes. In fact, the lack of governmental oversight caused the competing canneries at Karluk to self-regulate the salmon fishing in 1890, though many conflicts still occurred between the different beach seine crews:

> [Karluk Spit, 1890] That fishing at Karluk had interested a lot of cannerymen. There was twenty-seven seines in on that one seining ground there in 1890. And there wasn't a single law enforcement official. Later I read that Congress passed the first legislation limiting the methods of fishing in the Territory in 1888–89. They had a few revenue cutters around up there, coming and going, trying to figger out about it all. But we never heard of no laws. We didn't have no one to tell us what to do. There we was, out of touch with everyone, all trying to fish at the same time in the same place. It's a wonder there wasn't more shooting than there was. Why, so many fellows waited to fish, that as quick as the end of one seine was pulled up on shore, another outfit would throw in. . . . Finally, the cannery representatives called a meeting . . . The law we agreed on was this: no one could fish on Saturday. . . . The next law was that the cannery representatives would meet every Saturday night and shake dice to see who would get the first haul . . . The year after that the government took over. The boys said it was all right as long as the revenue cutters was there, but as soon as a cutter was

[28] 1) Ball, E. M. 1916. Report of operations, July 21, 1916. Unpubl. report. 1 p. Located at NARA, Anchorage, AK.
2) Memo reports (27 April and 23 July 1916) from E. M. Ball, Assistant Agent, Alaska Fisheries Service, USBF, Washington, DC, to Commissioner of Fisheries, Washington, DC. Located at Alaska Historical Collections, Alaska State Library, Juneau, AK.
3) Ball, E. M. 1917. Extract semi-monthly report of Mr. E. M. Ball, season of 1917. Unpubl. report. 1 p. Located at NARA, Anchorage, AK.
4) Ball, E. M. 1919. Extract from report of Mr. E. M. Ball, season of 1919. Unpubl. report. 3 p. Located at NARA, Anchorage, AK.

gone, one of the canneries would anchor a boat on the seining grounds. (McKeown, 1960)

In 1891 the eight canneries taking sockeye salmon at Karluk formed the Karluk River Fisheries, a cooperative agreement that controlled the fishing and apportioned the resulting case pack (Roppel, 1986). J. K. Luttrell, special agent of the U.S. Treasury Department, recommended in 1893 that a federal officer be posted at Karluk during the fishing season to enforce the laws, but this was not done (Luttrell, 1898). In the summer of 1914, E. Lester Jones, USBF Deputy Commissioner of Fisheries, toured coastal Alaska and was appalled by the lack of governmental regulation of the salmon fisheries, a shortcoming previously noted in 1897 by David Starr Jordan and C. L. Hooper (Jordan and Evermann, 1904). In particular, these men stressed the critical need for a fleet of federal patrol vessels to help fishery regulatory agents perform their enforcement duties:

[Alaska, 1914] A fundamental necessity in the protection of the fisheries of coastal waters is a fleet of vessels of a type fitted for the requirements of the region concerned. . . . It is absolutely necessary to have more boats and funds to carry out the instructions of Congress in regard to the enforcement of the fishery laws of Alaska . . . Without more vessels and men it is almost .. useless to make laws to protect this great fishing industry . . . The waters to-day in western Alaska, including the fishing districts of . . . Kodiak Island .., are practically without any protection, and fishermen operate in any way they care to, without, I may say, even the slightest semblance of investigation or restriction. This is entirely due to the fact that there are no Government vessels to look after these vast and important fields. We have one man stationed at Afognak Island, not only an isolated place, but with the waters surrounding it and Kodiak Island treacherous and dangerous a greater part of the time, and all we have available for his use is an 18-foot skiff. In this he is supposed to investigate fishery violations and follow fast-moving tugs and fishing boats. As a result, this Government official has been forced to jeopardize his life by going out in this skiff, or resort to the unfortunate and inexcusable practice of asking a cannery to furnish passage on a boat so that he may investigate the company's own fishery operations. This is the only safe means he has of getting there. The necessity of such a practice is ludicrous and absurd in the performance of official inspection work. To cite one instance which reflects discredit on the Government: One of our chief officials in Alaska requested that a cannery tug take him to a certain fishing ground so that he might see if the law was being violated. The company's superintendent readily acquiesced, and when he was nearing the fishing grounds blew five long blasts. The Government official naturally inquired why this was done, and the answer came back: "I am very sorry, but my instructions from the boss are to warn all the fishermen by five whistles when any of our boats are carrying a United States fisheries official." In other words, they were in the habit of violating the law and this was a warning that they must desist for the time being. (Jones, 1915)

U.S. Bureau of Fisheries patrol vessel, *Blue Wing,* 1947. (E. P. Haddon, National Oceanic and Atmospheric Administration Photo Library, ship0313)

His recommendation of seaworthy patrol vessels eventually was fulfilled by the USBF in the 1920s. Thereafter, several USBF vessels—*Blue Wing, Brant, Crane, Eider, Penquin, Red Wing,* and *Teal*—patrolled the coastal waters of Kodiak Island to monitor the fishery or passed through the region en route to the Aleutian and Pribilof islands.

During the early fishery, the number and location of canneries that harvested sockeye salmon from the Karluk system varied substantially (Fig. 2-2). After the initial proliferation of five canneries on or near Karluk Spit in 1882–89—from west to east: 1) Alaska Improvement Company, 2) Karluk Packing Company, 3) Aleutian Island Fishing and Mining Company, 4) Hume Packing Company, and 5) Kadiak Packing Company—all of these were consolidated into the APA facilities or closed by 1897 (Roppel, 1986). In addition to the five Karluk Spit canneries, another three canneries located further from Karluk also took sockeye salmon from this system—Arctic Packing Company on Larsen Bay and Royal Packing Company and Russian–American Packing Company on Afognak Island. When Afognak Island was set aside as a Forest and Fish Culture Reserve in 1892, its two canneries were closed.

The APA continued to operate several Karluk Spit canneries during 1897–1910, but closed them all after

Wreck of the Alaska Packers Association ship *Servia,* Karluk, 6 November 1907. (John N. Cobb, University of Washington Libraries, Special Collections, UW 14295)

they built a new cannery at Larsen Bay in 1911. Karluk Spit, the main site where fishermen caught sockeye salmon with beach seines, had major disadvantages for cannery operations, including an unprotected anchorage and lack of deep-water access for large vessels. These physical limitations had plagued the APA for many years and greatly complicated their work. Since large vessels drawing more than 1.2 m of water could not dock at the Karluk Spit canneries, it was often difficult to transfer supplies and passengers, and the entire case pack of salmon had to be lightered in small boats to the ships lying offshore in Shelikof Strait, fully exposed to sudden storms and rough seas that threatened to drive them onto the nearby rocky coastline.

During the early era when sailing vessels supplied the Karluk Spit canneries and received their output, the exposed anchorage resulted in a succession of disastrous shipwrecks—schooner *Pauline Collins* (6 October 1881), bark *Julia Foard* (27 May 1888),[29] ship *Raphael* (7 July 1895), bark *Merom,* (6 October 1900), and ship *Servia* (6 November 1907). Additionally, several smaller launches were wrecked at Karluk (U.S. Senate, 1912)—*Annie May* (1895), *Karluk* (1899), and *Delphine* (1903). Between 1888 and 1907, shipwrecks at Karluk and around Kodiak Island cost the APA about $658,000. These losses and other problems with the Karluk Spit site finally convinced the APA to replace the existing facilities with a single, large, new cannery at Larsen Bay, a protected location for vessels on the west side of Uyak Bay and 29 km east of Karluk. Work on the new cannery began in 1909 and was completed in time to process the 1911 salmon harvest (Marsh and Cobb, 1911). Commercial fishermen continued to beach seine for sockeye salmon at Karluk Spit for many years, but the harvested salmon were then transported 47 km by sea to the new cannery.

Charles H. Gilbert

1917–27

Charles Henry Gilbert began his studies of Karluk's sockeye salmon about 1917, during the last 10 years of his distinguished career as a descriptive ichthyologist,

Charles Henry Gilbert (1859–1928). (From William W. Gilbert, deceased)

[29] Some references say the *Julia Foard* (or *Ford*) was wrecked at Karluk on 27 April 1888.

pioneering fishery biologist, and educator (Dunn, 1996, 1997). From 1891 until his retirement in 1925, Gilbert was Professor and Chairman in the Department of Zoology, Stanford University. Prior to 1909 he collected and described hundreds of freshwater and marine fishes, mainly from the American west and Pacific Ocean. Several early collecting trips brought him to Alaska, where, in 1903, he served as a member of the Alaska Salmon Commission, being stationed at Bristol Bay. Gilbert, an authority on Pacific salmon, was appointed Scientist-In-Charge of USBF Pacific Coast fisheries in 1909, and thereafter focused much of his attention on the biology of salmonid fishes (Dunn, 1996). In about 1909–12, he first began using fish scales to age Pacific salmon and study their racial composition.

Because of Gilbert's extensive knowledge of Pacific salmon, his previous travels in Alaska, and his contacts with other salmon biologists, he undoubtedly knew about Karluk's abundant runs of sockeye salmon and intense commercial fishery well before he began studies there. Yet, it remains unclear just when Gilbert first visited Karluk. He analyzed a few hundred scales of Karluk's adult sockeye salmon collected in 1914, 1916, and 1917, most likely by various USBF workers (Gilbert and Rich, 1927).[30]

Gilbert annually visited Alaska to study salmon during 1917–27 (Dunn, 1996) and in 1919 he spent two days (25–26 July) at Karluk Lake with Henry O'Malley, then USBF field agent in charge of Pacific Coast operations. They limited their explorations to the north end of Karluk Lake. From this brief survey, they concluded that Spring, Moraine, and Cottonwood creeks were rather poor spawning habitats for sockeye and suggested that a hatchery at the lake may be beneficial (Gilbert and O'Malley, 1920). Their report to Commissioner of Fisheries Hugh M. Smith warned about overfishing of sockeye salmon and urged greater governmental protection for the Karluk River and other salmon streams in central and western Alaska. Further, they called for increased scientific studies of Alaska's salmon and emphasized the vital importance of collecting escapement and other fisheries data. Gilbert understood in 1919 that Pacific salmon returned to a home stream and that proper management and conservation must be based on fisheries data collected at each river system.

To obtain these fisheries data, the USBF, at Gilbert's direction, operated a counting weir on the lower Karluk River in 1921 and for the first time accurately measured the escapement of adult sockeye salmon to the spawning grounds. This first counting weir in Alaska came from Gilbert's recognition that escapement and other statistical data were urgently needed to understand the life cycle and population dynamics of sockeye salmon.[31] By combining the escapement and catch data, the total run of sockeye salmon was correctly determined for the first time at Karluk in 1921. Without a doubt, the weir operations provided vitally important data on Karluk's sockeye run and 1921 marked the beginning of a sustained program of biological studies on this salmon species.

Henry O'Malley (1876–1936). (From 1922 *Pacific Fisherman* 20(6):16)

Besides the actual counts of escaping sockeye, other fishery data were collected at the weir. Although few scales were collected from adult sockeye salmon in 1921, hundreds of samples were soon taken each year and analyzed to learn the abundance and age composition of the run. Information was also recorded on fish size and sex. With these new data Gilbert began exploring the stock-recruitment relationship of Karluk's

[30] USBF. 1914. Karluk River scales. Unpubl. data. 7 p. Located at NARA, Anchorage, AK.

[31] USBF officials Henry O'Malley, Field Agent; Ward T. Bower, Chief Agent, Alaska Service; and Hugh M. Smith, Commissioner of Fisheries, were also instrumental in establishing the Karluk River weir.

sockeye salmon, though answers were still years away because of the complex and long life cycle. He felt that management of sockeye salmon would be improved once the relationship between escapements and returns was known. Apparently these new data collections and research ideas were initially viewed with skepticism or humorous derision by some governmental and cannery workers. For the next 15 years, Karluk's research biologists were affectionately called "the Bug Hunters," possibly in reference to the hordes of mosquitoes and flies they had to endure to collect the fisheries data.[32] Nevertheless, collection of escapement and run composition data is now a routine annual task for fishery biologists; these data monitor natural population fluctuations, guide management policies, and check rehabilitation efforts.

Following his 2-day incomplete visit of 1919, Gilbert made a second short reconnaissance of Karluk Lake on 8–12 August 1921 with O'Malley, Fred Lucas (USBF fish culturist at Afognak Hatchery), and "Mose," a resident of either Larsen Bay or Karluk Village.[33] Departing from Larsen Bay cannery, they traveled to Dreadnaught City (a few cabins) at the head of the bay, packed across the portage trail, and then continued upriver by boat to Karluk Lake, camping the first night at Tent Point. Over the next four days, they circumnavigated Karluk Lake by boat, proceeding first along the west shore to the lake's southern end and into O'Malley Lake. They stopped at tributaries entering the lake and explored upstream, noting the abundance and condition of spawning sockeye and the creek's physical features (water depths, substrates, and water temperatures). Salmon were also seen spawning at several locations along the lake's shoreline. At the outlet of O'Malley Lake, Mose shot a large eagle that was distinctly different than the common bald eagle. Gilbert (1922) later published a short note on this unusual bird of prey, a Steller's sea-eagle, *Haliaeetus pelagicus.*[34]

Continuing their explorations, the party traveled north along the lake's east shoreline and into the Thumb Lake drainage. At Thumb River, Gilbert found a dead male sockeye of only 200 mm length, but this small fish had mature testes. Finally, they traveled north from the Thumb River and examined several more tributaries, completing their investigation of Karluk Lake. During this circumnavigation, they occasionally took depth soundings in Karluk, O'Malley, and Thumb lakes, and Gilbert began naming prominent shoreline landmarks. They left the lake on 13 August and floated the full length of the river to the new counting weir near Karluk Lagoon.

Gilbert made a third brief survey of the sockeye spawning grounds at Karluk Lake on 18–28 August 1922. The survey crew included Gilbert, his USBF assistant Willis H. Rich, William P. Studdert, and Fred R. Lucas (Superintendent of Afognak Hatchery). The trip from Larsen Bay to Karluk Lake was particularly tiring and time-consuming in 1922. From the APA Larsen Bay cannery, the party traveled by boat to the head of the bay, where six natives packed their gear across the portage trail. Proceeding upriver in an outboard-powered skiff, they went only 3 km before the shallow water rendered the motor useless. They then rowed and pulled the boat 10 km upstream against swift currents, but their progress was slowed by the mounds of gravel pushed up in salmon redds, forcing the party to spend a night on the upper river.

Reaching Karluk Lake the next day, the group erected a tent camp on Camp Island, from which they traveled around the lake for the next week. Again, they noted the abundance of spawning sockeye and explored each tributary upstream to impassable falls or natural salmon barricades. Fewer sockeye were present in the tributaries than in 1921, but they observed fish spawning in the upper Karluk River. Unexpectedly, pink salmon were discovered in some lake tributaries. Gilbert and Rich named many of the lake's landmarks and tributaries in 1922. The survey party floated downriver to the weir on 25 August (a trip of about eight hours) and found it partially washed out, damaged by the masses of pink salmon carcasses that had drifted downstream.[35]

On the regulatory front, the first use of weirs at Karluk and other Alaskan rivers was soon followed by passage of the federal White Act of 1924. This law mandated that 50% of the total salmon run must be allowed to

[32] J. Thomas Barnaby 1930–37 notebooks. Located at NARA, Anchorage, AK.

[33] Charles H. Gilbert 1921 and 1922 field diaries. Location of original field diaries at Stanford University Libraries, Department of Special Collection and University Archives, Palo Alto, CA; typed summary of Gilbert's trips to Karluk Lake at NARA, Anchorage, AK.

[34] Friedmann (1935a) identified the bones of Steller's Sea Eagle from prehistoric sediments of an archaeological excavation made a short distance from the Karluk River watershed. He concluded that this species was a casual visitor to Kodiak Island (Friedmann, 1935b).

[35] Details of the 1921 and 1922 field trips to Karluk Lake can be found in Gilbert and Rich (1927), and in the 1921 and 1922 field notebooks of Charles H. Gilbert (See footnote 33) and Willis H. Rich (1922). Location of copies of Rich's notebook at NARA, Anchorage, AK, and ABL Library, Auke Bay, AK.

escape the fishery; this requirement was monitored for compliance during the run season by closely comparing the weir counts and harvest data. It was assumed that if this proportion of the total run reached the spawning grounds at Karluk Lake each year, the salmon fishery would be placed on a sustainable basis. It was also in 1924 that the commercial fishery began using stationary ocean traps to capture sockeye salmon along the northwest coast of Kodiak Island (Rich and Ball, 1931).

Though Gilbert regularly traveled to Alaska for several more years and often visited Larsen Bay or the Karluk River weir, apparently 1922 was his last trip to Karluk Lake. In 1925 he briefly worked at the weir in June, collecting Dolly Varden scales and sockeye salmon smolts. He also completed two tagging studies in 1925–26, measuring the travel times of adult sockeye in the Karluk River. In the first study in August 1925, he tagged and released 200 adult sockeye off Karluk Spit and then observed their passage of the lower river weir. For the second study in July 1926, he tagged 100 sockeye at the lower river weir and measured their passage of the Portage weir (Gilbert and Rich, 1927). Although not a direct Karluk study, in the early 1920s Gilbert also did several ocean-tagging studies of sockeye salmon in the waters south of the Alaska Peninsula; significantly, he showed that salmon made long-distance ocean migrations and were not just restricted to their home stream vicinity.

Gilbert remained in charge of the sockeye research program at Karluk until 1926, when Willis Rich was given this responsibility. Notwithstanding this leadership change, Gilbert's influence continued for at least the next two years, and the research ideas for Karluk came from both men. Rich obviously respected Gilbert's knowledge and often sought his advice. When Gilbert visited Larsen Bay in 1926 and 1927, Rich specifically went there to discuss the Karluk studies. In 1926 Rich began an ambitious long-term study of the ocean survival of Karluk's sockeye by annually marking and releasing about 50,000 smolts. It is unclear if Gilbert designed this ocean survival study, but it appears likely he was heavily involved because of his intellect, ideas, and dominant personality. His research interests were then focused on Alaska salmon, and as recently as 1925 he had personally collected sockeye smolts at the Karluk River. In any event, Gilbert planned to accompany Rich to Karluk Lake in 1926 and 1927, but declining health prevented him from making the strenuous trip. Barnaby (1944) eventually published the ocean survival research that began during Gilbert and Rich's tenure at Karluk, for the first time documenting that its sockeye salmon had much higher survival rates than expected.

Biological knowledge of Karluk's sockeye salmon greatly advanced under Gilbert's leadership of the research program. Significantly, his discoveries were based on solid scientific data obtained by the annual operation of the counting weir, the regular sampling of the adult and smolt runs, and the examination of scales that revealed the stunning diversity of freshwater and ocean ages present in the run (Gilbert and Rich, 1927). Though such fisheries data are routinely collected nowadays, these were significant accomplishments in the 1920s. Major discoveries on sockeye salmon biology during Gilbert's tenure as research leader at Karluk included the following topics:

1) Escapement numbers reaching the Karluk Lake spawning grounds.
2) Total run size.
3) Seasonal distribution of the run.
4) Number of years spent in the freshwater and ocean.
5) Diversity of age groups present in the run.
6) Seasonal variation in age composition, size, and sex ratios of the run.
7) Timing of downstream smolt migration.
8) Stock-recruitment relationship.
9) Abundance and run timing of other salmonid species.

In conclusion, Gilbert's studies of sockeye salmon at Karluk started the long-term collection of detailed fisheries data that has continued without interruption to the present. While he spent most of his career as a descriptive ichthyologist, it is remarkable that the research he pursued at Karluk falls within the discipline of fishery biology, topics that remain important to current biologists. Although much of Rutter's work at Karluk in 1903 would also be classed in this discipline, Gilbert is often considered the intellectual founder of fishery biology in the U.S. (Dunn, 1996).

Willis H. Rich

Willis Horton Rich maintained an interest in Karluk River sockeye salmon for over 25 years, a long episode that included his direct field research during 1922–32 and his later consulting work and critical reviews of USBF and FWS research programs. He actively led the sockeye salmon studies at Karluk in 1926–30, taking up these responsibilities from Gilbert. As significant as Rich's own field studies were at Karluk, he greatly influ-

Willis Horton Rich (1885–1972). (From 1925 *Pacific Fisherman* 23(12):21)

enced federal research on this system for many years, advancing ideas on the controlling factors of sockeye productivity and inspiring and advising several other Karluk biologists.

1922

Rich first visited Karluk Lake and River in the summer of 1922 as a USBF field assistant for Gilbert, then leader of the sockeye salmon studies. They surveyed the sockeye spawning grounds at Karluk Lake and examined the counting weir on the lower river. Though the trip lasted only 10 days (18–28 August), Rich (1963) became fascinated with the Karluk system and recorded many observations on its salmon, bears, flora, and physical landforms.[36] He prepared a rough map of Karluk Lake by taking bearings with a surveyor's compass and measuring base lines. With Gilbert, he named many of the lake's prominent landmarks and tributary creeks.

[36] Willis H. Rich 1922–1931 notebooks. Location of original notebooks unknown (in 1956, Rich had the original notebooks); copies at NARA, Anchorage, AK, and ABL Library, Auke Bay, AK. In 1963 the BCF ABL published the notebooks as a Manuscript Report.

Following his first brief visit to Karluk Lake and subsequent promotion to lead the USBF Division of Scientific Inquiry, Rich apparently did not return to Karluk during 1923–25, though he did travel to Alaska each field season to study other salmon fisheries. Rich earned his M.A. (1918) and Ph.D. (1924) degrees at Stanford University, with Gilbert serving as his major professor (Dunn, 1997).

1926

As the newly appointed leader of sockeye salmon research at Karluk, Rich spent the entire summer and fall of 1926 (23 May–24 September) at Karluk Lake and River, or nearby at Larsen Bay cannery. He collaborated with Gilbert on some field work that year, but also independently pursued many significant studies with his assistant Seymour P. Smith.

Marked smolts The 1926 field season was important in Karluk's fisheries history because, for the first time, Rich marked thousands of sockeye salmon smolts (by clipping various fins) for future identification when they returned as adults. Initially in 1926, Rich and Smith tried to collect smolts at the Karluk River Portage, but their sampling gear was poorly suited for that site. Moving operations downriver to the lower weir, they successfully marked and released 48,000 smolts during 30 May–16 June 1926. This ambitious mark-and-recapture experiment continued for the next 10 years; the annual smolt marking was the first step in measuring the ocean survival of sockeye salmon. To complete the experiment, Rich and his assistants searched through thousands of cannery-harvested adult salmon in subsequent years to find marked individuals (i.e. those missing various fins). This mark-and-recapture experiment was also designed to accurately measure total smolt out-migration each year, but for unknown reasons this part of the study was never completed.

Smolt observations As Rich marked the sockeye smolts, collected their scales, and measured their lengths, he soon learned that larger and older smolts dominated the early migration, the size and age decreasing with time. Overall, he was impressed by the large size of Karluk's sockeye smolts:

> [Speaking of Karluk's sockeye salmon smolts, 1 June 1926] These migrants are certainly very fine fish—by far the finest I have ever marked and I should not be surprised if we received a high percentage of returns.

> Judging by the results of the best marking experiments in the Columbia River it would not surprise me if we got as high as 10% from these.[37]

The downriver smolt migration lasted about three weeks; the fish moved downstream in pulses, being abundant for several days and then absent for a few days. He also noted their nocturnal migratory behavior. The work of capturing and handling 48,000 smolts gave him data on the proportion of fish with naturally missing fins and the presence of parasitic copepods attached at the base of ventral fins. Further, he recorded the presence of coho and Chinook salmon juveniles.

Adult sockeye behavior at the weir During the three weeks that Rich marked smolts at the Karluk River weir, he closely observed the upstream migratory behavior of adult sockeye. Contrary to past criticisms that the weir harmed migrating adults by preventing their upstream progress, Rich concluded that the weir was not a serious obstacle. He saw that when adult salmon were ready to move upstream, they easily found the open counting gates and passed through the weir.

Salmon travel time up the Karluk River Two counting weirs were operated on the Karluk River in 1926, one on the lower river near Karluk Lagoon and another 20 km upstream at the Portage. Adult spring-run sockeye were marked at the lower weir and their passage was recorded at the upper weir. These salmon needed 4–5 days to travel this distance and about one week to reach Karluk Lake (Gilbert and Rich, 1927).

Exploration of the spawning grounds and observation of the large escapement The 1926 field season was important for Rich because he observed one of the largest runs of adult sockeye salmon at Karluk since commercial fishing began in 1882. In 1926 over 2,500,000 sockeye escaped to the spawning grounds from a total run of over 4,500,000, a huge run never repeated again in the subsequent 80 years. Possibly, Rich may have been the only trained fishery biologist ever to observe a Karluk sockeye run of similar magnitude to those existing before or shortly after commercial fishing began.

Rich was impressed by the number of sockeye salmon flooding onto the spawning grounds, the sight forever affecting his ideas about Karluk's productivity. He regularly traveled around the lake in 1926, visiting the spawning tributaries and beaches, exploring upstream along tributaries, and noting the numbers of dead and live sockeye.[38] Often, tributaries were densely packed with spawning adults or littered with decomposing carcasses. The number of spawners decreased in August, but Rich saw many adult salmon swimming in the lake, causing him to theorize that a certain lake-ripening period was needed before these fish moved to specific spawning sites. He saw that fall-run sockeye were larger than spring-run fish. On a trip downriver on 27 August, he observed many adult sockeye spawning in the first 3 km of river below the lake.

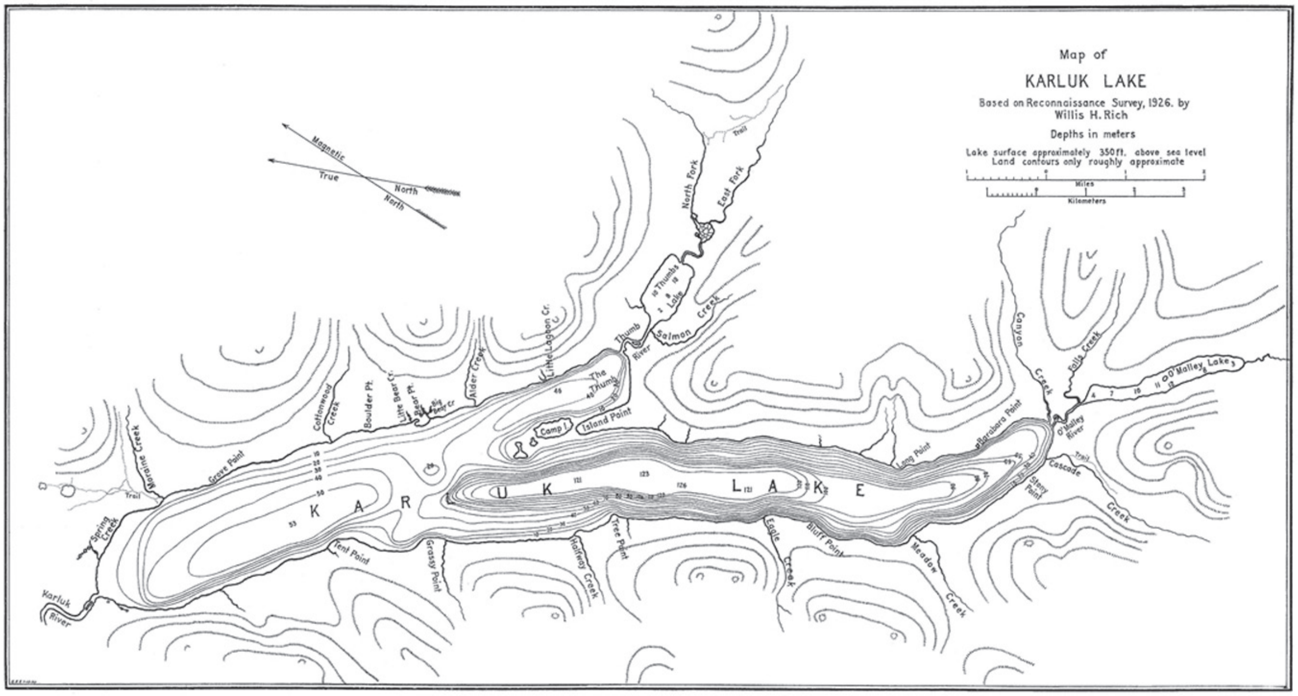
Sockeye carcasses and Karluk Lake's productivity While surveying the spawning habitats at Karluk Lake during July–August 1926, Rich was constantly impressed by the huge numbers of sockeye carcasses present, these even being transported by stream currents and lake waves far from active spawning sites. He observed the rapidity of carcass decay and the action of blowflies in the breakdown. Significantly, on 9 August he noticed a dense phytoplankton bloom in Thumb Lake and linked this to the nutrients that leached from decaying salmon carcasses. He soon realized the possible importance of salmon-carcass nutrients to Karluk Lake's fertility and the sustenance of juvenile sockeye. His 1926 observations at Karluk Lake marked the origin of the theory that salmon-carcass nutrients influenced the lake's productivity and sockeye salmon abundance, an idea that has persisted to present times.

Bathymetric map of Karluk Lake Rich prepared the first detailed bathymetric map of Karluk Lake using a sextant, plane table, aneroid barometer, and sounding line (Gilbert and Rich, 1927). The map showed the lake's three internal basins. He also mapped the two shallow lakes (Thumb and O'Malley) tributary to Karluk Lake. The map aided his future limnological studies of Karluk Lake.

Limnological measurements of Karluk Lake In 1926 Rich collected the first limnological data from Karluk Lake, thus beginning a regular sampling program that, with alterations and interruptions, can be traced to today's limnological monitoring. Rich measured the surface temperatures of Karluk, Thumb, and O'Malley lakes and tributaries, and ran temperature profiles in all three basins of Karluk Lake. In addition, he collected plankton samples, measured water trans-

[37] See footnote 36.

[38] In 1926 Rich spent over a month at Karluk Lake observing sockeye salmon (27–28 June, 12–22 July, and 29 July–27 August).



Bathymetric map of Karluk Lake, showing three internal basins, tributary streams and lakes, and landmarks. (From Gilbert and Rich, 1927)

parencies, and retrieved bottom sediments, though these were largely preliminary efforts at testing the effectiveness of his sampling gear. To monitor changes in the lake's water level, he engraved a permanent benchmark on a rock outcrop at Camp Island.

Salvage of wasted sockeye eggs As Rich and Smith surveyed the spawning habitats at Karluk Lake in 1926, they found many dead, unspawned, sockeye females. Rich was unsure if these premature deaths resulted from the excessively large escapements flooding onto the spawning grounds, the relatively dry summer and reduced water levels, or other factors. Nevertheless, he believed that the unspawned eggs were a regrettable waste of reproductive products and calculated the untold millions of lost eggs. Thinking that dead unspawned females might be a regular feature of the Karluk system and not unique to 1926, he devised a plan to salvage the wasted eggs by culturing them in a lake hatchery. Eggs in dead females seemed to be in good condition for artificial propagation. Testing the idea, he gathered eggs from dead and live females, fertilized and buried them in the substrate, and checked their progress for several weeks. Test results were mixed, but some eggs from dead females developed normally, and Rich concluded "that the eggs from dead females may be successfully fertilized and will pass through at least the early stages of development as well as those from living females. I have no doubt, of course, but that the eggs must be taken before the females have been dead too long ."[39] Yet after spending a few more field seasons at Karluk without again finding dead unspawned females, Rich realized the 1926 conditions were unique and never pursued the hatchery idea. The presence of unspawned females indicated, however, that Karluk's spawning area might be limited and that the spawning capacity was exceeded by the huge escapement of 1926. Nevertheless, though these unspawned females did not contribute to egg seeding and fry production at Karluk, they did add salmon-carcass nutrients to the lake and possibly increased the success of juvenile sockeye.

Sockeye fecundity Just before Rich ended the 1926 field season and left Alaska, he collected eggs from 40 adult sockeye females at Larsen Bay cannery in mid September. From this small sample he obtained a fecundity estimate for fall-run sockeye and learned how fecundity varied with female size (Gilbert and Rich, 1927).

Fry growth rate in Karluk Lake As Rich and Smith traveled around Karluk Lake in 1926, they constantly looked for juvenile sockeye and tried to learn about

[39] See footnote 36 (8 August 1926).

their habitats, growth rates, and food habits. Such data were needed to understand the full life history of Karluk's sockeye salmon and were of special interest to Rich and Gilbert in interpreting scale ages. When the 1926 field season began, they had two specific questions about juvenile sockeye: 1) do any fry emerge and form scales in the same year as egg deposition, and 2) do fry emerge early enough in spring or summer to grow and form scales with circuli? Rich concluded that, "in view of the low temperature recorded on the main spawning streams it seems very unlikely that any of the young salmon hatch and come out of the gravel before spring . . ."[40] He also learned that juvenile sockeye grew and formed scales in their first year following spring emergence. But attempts to catch juvenile sockeye with beach seines were largely unsuccessful in 1926 and Rich planned to use other sampling methods in 1927.

Charr observations Rich examined the food habits and reproductive condition of Karluk's charr in 1926, though it was not yet known that two species were present in this system. All charr at Karluk were then called "Dolly Varden," and they were thought to be serious predators of salmon eggs and young. Rich examined 105 Dolly Varden from the lower Karluk River on 1 June, finding all had empty stomachs and immature gonads. Two months later (8–9 August) he saw many large Dolly Varden feeding on sockeye eggs in the Thumb River and in streams at the south end of Karluk Lake. These brightly colored fish had well-developed gonads and were preparing to spawn. Rich was unconcerned about the egg consumption, stating that "these eggs form the chief food for the dollies at this time, but they are eggs that would be wasted anyway so that no harm is done by the dollies in feeding on them."[41]

Pink salmon A huge run of pink salmon entered the Karluk River in 1924, and many of these reached the lake spawning grounds. Possibly, these pink salmon may have harmed the sockeye by spawning in the same tributaries, digging up previously buried sockeye eggs and depleting oxygen concentrations that killed fish in these small creeks. After the large pink salmon run at the lake in 1924, a similar large run was expected in 1926, and the USBF made plans to protect the sockeye salmon spawning streams. Initially, Rich wanted a weir placed at the lake's outlet to bar pink salmon, but this was logistically impossible. His second plan was to install small wire weirs at sockeye spawning streams to block the pink salmon. But, in fact, the 1926 pink salmon run was small and Rich concluded in late July "that it will not be necessary to put in the web weirs at the mouths of the stream entering the lake unless a much heavier run of fish comes in."[42]

Scale collections Rich and Gilbert collected and read sockeye salmon scales at Larsen Bay and Uyak canneries in May 1926. Rich declared that the scales he examined at Larsen Bay were "the first opportunity I have ever had to examine red salmon scales in any quantity."[43] When Rich and Smith examined sockeye scales at the canneries in early July, they concluded that some of these could not be from Karluk River fish:

> [Larsen Bay cannery, 3 July 1926] S. and I examined the scales from the few reds we got in Larsen Bay on the 3rd and it was very clear that there was a race of fish present which was quite different from the fish of the Karluk River. Out of 16 examined 4 were apparently Karluk River fish but the other 12 were quite certainly of a very different race. These fish have a very small [nucleus] 1 year in the freshwater and most of ours are 5-year fish. The difference in the freshwater growth of these fish and those from Karluk is as distinct as anything of the sort I have ever seen.
>
> [Uyak cannery, 8 July 1926] . . . . we examined the rest of the scales taken from the gill net fish. Found that those taken in the Bay were very similar to the few trap fish in Larsen's Bay; i.e., they contained a large percentage of fish 5_1 and with very similar [nucleus], a race quite distinct from the Karluk River fish.[44]

When Gilbert left Alaska in July 1926 for health reasons, he asked Rich to collect sockeye scales at Karluk Lake and the canneries, and from grilse in the fall-run sockeye. Rich managed to obtain the grilse scales in early September, but found little time to collect scales at the spawning grounds and questioned the value of such samples:

> [Karluk Lake, 22 August 1926] Our collection of scales from tributary streams as desired by Dr. G. has practically fallen through . . . . Since we came back [to Karluk Lake] it has been almost impossible to do anything in the way of collecting the data on account of the mixture of fish of the early run and those of the later run which, of course, show differences in size on account of the longer time spent in the o. [ocean] by the later running fish. In my opinion unless one is careful

[40] See footnote 36 (18 July 1926).

[41] See footnote 36 (23 August 1926).

[42] See footnote 36 (21 July 1926).

[43] See footnote 36 (24 May 1926).

[44] See footnote 36.

> to get representatives from the different tributaries for the small run of fish there is great chance for serious confusion due to the various mixtures of fish of the different runs.[45]

Observations of aquatic flora and fauna Besides his sockeye studies, Rich observed and collected other species of the flora and fauna at Karluk, including aquatic macrophytes and macroinvertebrates. Likewise, Rich and Smith somehow found time to collect and preserve bird eggs for Harold Heath of Stanford University. In exploring this non-fisheries information, Rich was somewhat unique among Karluk's biologists.

Rich and Smith's research accomplishments at Karluk in 1926 were substantial, especially considering the time they spent doing all the necessary practical things to survive and travel in this remote region. For example, early in the field season as they marked smolts at the weir they found scant living accommodations in the abandoned and dilapidated APA hatchery building. After hatchery operations had ceased in 1916, the building's lumber and other parts had been scavenged in the intervening 10 years. In addition, rough seas in Shelikof Strait often prevented boats from landing at the exposed Karluk Spit, making travel and landing supplies tenuous. Once supplies were ashore, they were transported up the shallow estuarine waters of Karluk Lagoon in a small skiff, this travel being easiest at high tide. Fairly modern accommodations then existed at Larsen Bay cannery, and ocean travel around Kodiak Island occurred on USBF patrol vessels or commercial fishing boats.

Yet, travel to Karluk Lake remained nearly the same as when Rich last visited in 1922. This involved an ocean boat trip to the head of Larsen Bay, a strenuous pack of supplies across the portage trail to the Karluk River, and then 14 km of upriver travel in a small skiff. In 1926 the USBF leased a small homestead with several cabins (humorously called Dreadnaught City) at the head of Larsen Bay, and Rich used the cabins to store supplies and as temporary shelter while traveling to and from the lake. Also in 1926 the USBF built a new weir cabin at the Karluk River Portage, this giving another shelter when making trips between the lake and Larsen Bay. Ascending the Karluk River was seldom easy, and the low water of 1926 made it difficult to haul the heavy supplies, scientific gear, and lumber. An outboard motor powered the skiff in the deep water near the Portage, but for most of the trip, the boat was manually pulled upstream in the shallow water, often through rainstorms and hordes of harassing insects.

Since no cabins existed at Karluk Lake in 1926, Rich erected a tent camp on Camp Island, first building a level wooden floor. Though the tent gave tolerable shelter, he still wanted a cabin for future salmon research at the lake. During travels to and from the lake, Rich and Smith occasionally found shelter in a native barabara, one being located near the lake's outlet and another near the Portage. While staying at Camp Island, they supplemented their provisions with fresh fish and waterfowl. When Rich and his field crew left Karluk Lake to float downriver to the Portage on 27 August, the normally easy trip going with the current lasted 6.5 hours, the river being so low they had to drag the boat downstream.

In conclusion, Rich and Smith had a productive field season at Karluk in 1926, and their results greatly increased the knowledge about sockeye salmon. They initiated several studies of sockeye salmon that continued for many years, these long-term data being crucial to understanding this complex and diverse ecosystem. Equally important to the actual field work completed were the new research ideas generated in 1926 about the sockeye salmon's life history and the lake's fertility.

1927

Rich returned to Alaska in 1927 and spent considerable time in the Karluk–Larsen Bay area, including over a month at Karluk Lake.[46] Most of the studies that year continued those started in 1926, including marking 50,000 sockeye smolts at the weir, surveying the abundance of sockeye salmon on the spawning grounds, exploring salmon spawning streams, collecting limnological data at Karluk Lake, seining for juvenile sockeye, and examining charr food habits. Since sockeye salmon escapements to Karluk Lake were much smaller in 1927, Rich saw fewer adults and carcasses on the spawning grounds. Likewise, he found few unspawned dead females and abandoned his idea of salvaging unspawned eggs.

After his preliminary limnological work of 1926, it is likely that Rich was eager to collect further samples in 1927 to test his idea linking salmon-carcass nutrients and lake productivity. Consequently, besides having better collecting gear for plankton, bottom

[45] See footnote 36.

[46] In 1927 Rich was in the Karluk and Larsen Bay area on 26 May–31 August, and at Karluk Lake on 5 July–15 August.

sediments, water transparencies, and water temperatures, the 1927 studies included water chemistry measurements by George I. Kemmerer, Professor of Chemistry, University of Wisconsin. To learn if salmon carcasses affected the water chemistry of lake tributaries, Kemmerer and Rich compared nutrient concentrations above and below the upstream limits of salmon migration—lower stream sections had significantly higher nutrient levels.

To obtain water chemistry samples, Rich explored many tributaries much more thoroughly than before, finding that some had newly eroded channels. He collected plankton samples from Karluk, Thumb, and O'Malley lakes in 1927, and he again saw an August phytoplankton bloom in Thumb Lake, though it was less intense because fewer salmon carcasses added nutrients to the lake. It was not until 1932 that the limnological studies at Karluk Lake were published. This scientific paper, with Rich as a co-author, was the first to formally discuss the possibility that the fertility of Karluk Lake and success of juvenile sockeye were affected by nutrients leached from adult salmon carcasses (Juday et al., 1932).

Rich made a special effort in 1927 to collect young sockeye from Karluk Lake to determine their growth and food habits, but found it difficult to consistently capture juveniles in beach seines because the rough substrates often snagged his net. After selecting a smooth beach near Little Lagoon Creek, he collected about 200 juvenile sockeye, plus sticklebacks, sculpins, charr, juvenile coho salmon, and juvenile steelhead, and boasted that ". . .we have today caught more young *Oncorhynchus nerka* during their life in the lake than have ever been caught before".[47] He felt that this one sample was sufficiently large to understand the freshwater growth of juveniles.

The ocean migration routes of sockeye salmon that returned to spawn in Kodiak Island's streams were poorly known in 1927. Rich and Gilbert suspected that adult fish caught along the island's west coast, still far from the Karluk River, in fact homed to that river. To test this idea, Rich tagged and released 700 adult sockeye on 19–20 August at the San Juan #1 fixed trap located just inside Broken Point in Uganik Bay (Rich and Morton, 1930). His experiment showed that, indeed, most of these fish were of Karluk River stock. This result allowed the west coast fish to be more accurately assigned to their true natal stream, an important finding for management purposes.

[47] See footnote 36 (8 August 1927).

Rich found better lodging, travel, and survival logistics at Karluk in 1927. The best improvement at the lake was the 3.7 × 8.8 m cabin built on Camp Island in June 1927. This cabin was now the fisheries research base at the lake. The USBF also purchased the Dreadnaught City homestead and cabins in 1927 for $250. Cabins at Camp Island, the Portage, and Dreadnaught City aided the biologists as they traveled and hauled supplies to and from the lake. In contrast, worse living conditions existed at the weir on the lower river. Weir tenders had lived in the abandoned hatchery building since 1921, but it had deteriorated further each year and gave only marginal shelter. In 1927 Rich and his field crew camped in a small (3 × 5.5 m) wood shed while they marked sockeye smolts.

In 1927 the USBF provided the biologists with a Fordson track-laying tractor and sled, which made it much easier to haul supplies and travel across the portage trail between Larsen Bay and the Karluk River. Supplies were now transported by boat to the head of Larsen Bay, stored in the Dreadnaught City cabins, and hauled across the portage by tractor and sled to the cabin located on the river (then known as "Russellville"[48]). The Fordson tractor was often a mixed blessing for the biologists, being difficult to start, throwing off its tracks, and often sinking into the muskeg. From the Portage cabin, the trip upriver to Karluk Lake was made in a small boat driven by outboard motor, oars, and physical force. Henry O'Malley, then USBF Commissioner, wanted better access to Karluk Lake and proposed in 1927 the construction of a road across the portage and a trail to the lake. Fred Spach of the Alaska Road Commission made a reconnaissance survey of a possible road route in late August 1927. Though a road was never built, this idea continued for the next 20 years until air travel became the standard mode of transportation. Radio communication between Karluk Lake and Larsen Bay was attempted in 1927, but the equipment worked poorly.

1928–30

After their productive studies of Karluk's sockeye salmon during 1926–27, Rich and his assistants continued this research for the next three years. They started each field season by marking about 50,000 smolts, and then spent most of the summer looking for previously

[48] "Russellville" was a temporary name used by biologists for the cabin, boathouse, and few storage sheds at the Portage. It honored USBF employee J. R. Russell, who collected steelhead eggs at Karluk River Portage each spring during 1927–32.

marked adults at the canneries. Scales, length, and sex data were collected from sockeye smolts and adults to learn about their run compositions. Biologists visited Karluk Lake several times each field season to survey the sockeye spawning habitats and to collect limnological data. Juvenile sockeye were occasionally seined in the lake to learn more about their freshwater growth and foods.

Although Rich directed the studies during 1928–30, he spent less time at Karluk in those years.[49] In 1929–30 he helped mark smolts, looked for marked adults at the canneries, and visited Karluk Lake for 10 days each July. While marking smolts in early June 1930, Rich learned he was to be hired as a Professor of Zoology at Stanford University. Thus, after completing the 1930 field season, he resigned his USBF position as Director of Pacific Fisheries Investigations on 1 November 1930. Yet this change in employment did not end Rich's involvement with salmon studies in Alaska.

Little had changed in the transportation, living facilities, logistical supply, and communications for Karluk's fishery biologists during 1928–30. Travel to Karluk and Larsen Bay each field season required a 2-week ocean voyage from Seattle, Washington. USBF patrol vessels or commercial fishing boats provided local ocean travel between Karluk Spit and the canneries. Transport from Karluk Spit to the weir was by small skiff to the eastern end of Karluk Lagoon, though an alternate route occasionally used during rough ocean weather was to travel to the Portage and then float down the Karluk River. Since the APA hatchery building had been totally demolished by 1929, two small cabins were constructed near the weir. Travel to Karluk Lake continued to be the usual route across the portage by tractor and sled, and then by boat up the Karluk River. The Camp Island cabin continued as the fisheries research base at Karluk Lake.

1931–47

After 1930, Rich often returned to Alaska to continue his salmon studies, but he seldom visited Karluk Lake. His field assistant for 1930, Thomas Barnaby, was competent in doing the sockeye studies at Karluk and Rich expressed confidence that "Tom [Barnaby] is, as always, 100%".[50] Rich traveled to Alaska in 1931 with plans to visit Karluk Lake, but eventually relied on Barnaby to do the Karluk work, freeing him for other Alaskan studies:

> Shall not make the trip to Karluk Lake, much as I should like to do so, as I think my time will be better spent at Afognak and elsewhere and I know that Tom [Barnaby] will handle everything as well as though I were along.[51]

Rich's confidence in Barnaby came from working with him at Karluk in 1930 and at Stanford University. Likewise, Barnaby greatly respected Rich, once claiming that Rich had been the most positive influence on his fisheries career (Morton, 1980). This mutual respect was further demonstrated by the fact that Rich had collected the first five years of data for the ocean survival study (1926–30), but freely gave it to Barnaby, who published this information in 1944. Rich continued to give guidance to the sockeye studies at Karluk until 1932, often conferring with Barnaby about the work whenever they met at Larsen Bay.

Rich significantly influenced fisheries research at Karluk for many years beyond his direct involvement of 1926–30. He led the North Pacific Fishery Investigations for the FWS during 1943–44, and then served as a consultant for their salmon fisheries studies during 1944–50. In 1946 he reviewed a manuscript that FWS fishery biologist Richard Shuman had prepared for publication on the escapement-return relationship of Karluk's sockeye salmon. Rich strongly argued that the

Philip Aaron (left), Willis Rich (center), and Tom Barnaby (right), Karluk, 1930. (Joseph Thomas Barnaby, from Lynn L. Gabriel, Herndon, VA)

[49] Rich did not visit Karluk Lake in 1928, the entire field program being done by his assistants, Seymour P. Smith and Alan C. Taft. Rich visited the Karluk region in 1929 (25 May–25 July) and 1930 (23 May–20 July). His field assistants were Merrill W. Brown in 1929 and J. Thomas Barnaby in 1930.

[50] See footnote 36 (29 May 1930).

[51] See footnote 36 (16 July 1931).

historic decline of Karluk's sockeye was caused by nutrient depletion in the lake from loss of salmon carcasses to the commercial fishery. In contrast to Shuman's initial proposal for lower escapements goals at Karluk, Rich wanted higher escapements to reverse past nutrient losses. After Rich's critical review, Shuman added these nutrient depletion ideas into his manuscript and pursued limnological studies with renewed vigor, this work eventually leading to the fertilization experiment at Bare Lake in the 1950s. Rich continued to travel to Alaska in the mid to late 1940s, visiting Shuman and Nelson at Karluk Lake in August 1947 to discuss their research and the possible fertilization of the lake.[52]

Joseph Thomas Barnaby

1930–38

Joseph Thomas Barnaby first worked at Karluk in 1930 as a USBF assistant to Willis Rich. By then, he was well acquainted with field work in Alaska, having spent the previous five summers working at several private and USBF fisheries jobs at Prince William Sound and Southeastern Alaska. He had just earned his B.S. degree in fisheries at the University of Washington in 1929. Barnaby first met Rich in Alaska in 1929 and soon thereafter began graduate studies in zoology at Stanford University while working on Karluk's sockeye salmon.

Following Rich's appointment to Stanford University in late 1930, Barnaby was given full responsibility for the Karluk studies, though he continued to collaborate with Rich until at least 1932. Barnaby led the USBF fisheries studies at Karluk for nine years (1930–38), and his main research goals and field work continued those began by Gilbert and Rich in the 1920s—sockeye salmon ocean survival rates, description of run compositions, and limnology of Karluk Lake. His field seasons usually lasted from May through September,[53] the time being largely devoted to marking sockeye smolts, collecting scales, measuring fish, and looking for marked adults. But he also made at least two trips to Karluk Lake each year to continue the freshwater studies, which then comprised the limnological sampling, surveys and physical descriptions of the spawning habitats, and determination of juvenile sockeye growth and distribution.

Joseph Thomas Barnaby (1903–1998). (Joseph Thomas Barnaby, from Lynn L. Gabriel, Herndon, VA)

One of Barnaby's most important studies at Karluk was the measurement of sockeye salmon ocean survival, from the time when smolts entered the sea until they returned years later as mature adults. He determined this by first marking thousands of smolts and then recording the proportion of marked adults that returned in subsequent years. Each spring of 1930–36 as the sockeye smolts descended the Karluk River and accumulated above the weir, he captured, marked, and released about 50,000 fish, each year using a different combination of clipped fins. By mid June as the downriver smolt migration ended, Barnaby and his assistants shifted their efforts to searching for previously marked adult sockeye at the Larsen Bay and Uyak canneries, a massive effort that required the examination of thousands of harvested adult salmon.

From this data, Barnaby (1944) calculated smolt-to-adult survival rates of greater than 20%, consider-

[52] Richard F. Shuman 1947 notebook (3–7 August). Located at NARA, Anchorage, AK.

[53] Barnaby's Karluk Lake field work schedule: 22 May–20 Sept. 1930, 2 trips, 20 days; 10 April–30 Sept. 1931, 4 trips, 41 days; 22 May–22 Sept. 1932, 3 trips, 19 days; 17 May–2 Nov. 1933, 2 trips, 13 days; 11 May–15 Sept. 1934, 6 trips, 57 days; 8 May–16 Sept. 1935, 5 trips, 81 days; 21 May–21 Sept. 1936, 4 trips, 63 days; 31 May–25 Sept. 1937, 4 trips, 46 days; May–June 1938, number of trips and days unknown.

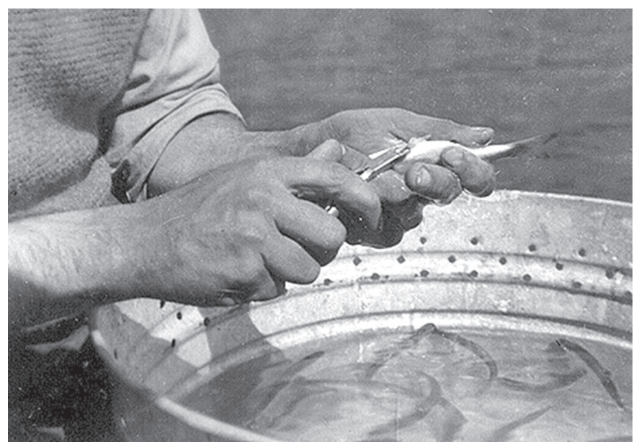
ably higher than had been previously reported for sockeye salmon.[54] An initial second goal of this mark-and-recapture experiment was to measure the total smolt out-migration, but for unknown reasons this part of the study was never completed or published. Barnaby understood the importance of knowing the yearly production of smolts from Karluk Lake, but apparently never calculated this abundance from the mark-and-recapture data.

A second important task that Barnaby and his assistants continued for nine years at Karluk was the regular collection of run composition data (age, size, and sex) from thousands of sockeye salmon smolts and adults. For the smolts, the ages and sizes of these young salmon changed during the 3-week out-migration, but males and females were equally abundant. The adult sockeye run, which lasted at least 4–5 months, also had seasonal variations in age, size, and sex ratio. Gilbert and Rich (1927) summarized the run composition data up to 1926, while Barnaby (1944) summarized it up to 1936. Furthermore, the run composition data were needed to calculate the ocean survival rates of sockeye salmon in the mark-and-recapture study. Besides these practical uses, the regular collection of adult scales in the 1920s and 1930s, from both the escapement and catch and over the complete migration season, led for the first time to an exquisite appreciation of the remarkably diverse and complex life cycle of Karluk's sockeye salmon. Thus, starting with the 1920s–1930s field work, it became a routine task for biologists to collect run composition data at Karluk, and these fisheries statistics have continued to be gathered nearly uninterrupted ever since.

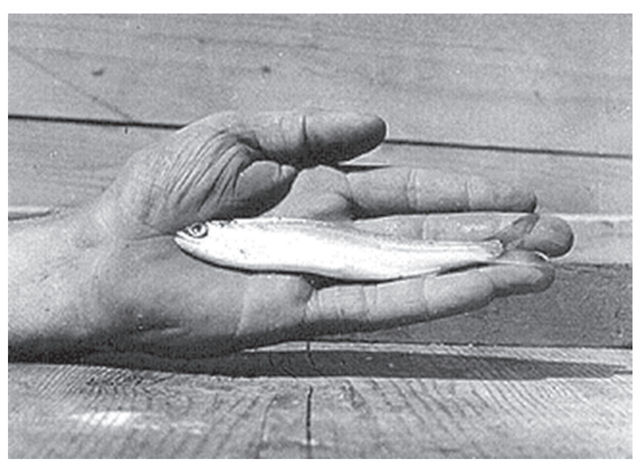
Barnaby completed his M.A. degree at Stanford University in 1932; for his thesis he investigated the relationship between body growth and scale size of Karluk's sockeye salmon in 1930–31 (Barnaby, 1932). To find out when scales first formed on young sockeye, he examined newly hatched alevins as they emerged from gravel redds and older juveniles during their early growth stage in Karluk Lake. Scales first appeared once feeding began, when juveniles reached about 36 mm in fork length (range 30–40 mm). From his 1930–31 field data and that collected by Rich in 1926–27, Barnaby discovered that a curvilinear relationship existed between fish length and scale size. Scales first grew faster than fish length, but later grew at a slower rate; a semi-

[54] Although smolts were marked yearly until 1936, Barnaby (1944) only analyzed ocean survival rates for those marked during 1926–33, possibly because recoveries of marked adults were not sufficiently complete for 1934–36.

Tom Barnaby (left) marking sockeye salmon smolts, Karluk River, 1930s. (Joseph Thomas Barnaby, from Lynn L. Gabriel, Herndon, VA)



Marking sockeye salmon smolts by clipping fins, Karluk River, 1930s. (Joseph Thomas Barnaby, from Lynn L. Gabriel, Herndon, VA)



Sockeye salmon smolt, Karluk River, 1930s. (Joseph Thomas Barnaby, from Lynn L. Gabriel, Herndon, VA)

logarithmic formula best fit the data. He determined precisely when juveniles and adults formed seasonal annuli on their scales. He also showed that the size of adult sockeye salmon was controlled by its length of ocean residence.

At Karluk Lake, Barnaby continued with the limnological work first began by Rich, who undoubtedly convinced him that lake studies were crucial for understanding the growth of juvenile sockeye. As a result, Barnaby collected limnological data for all nine years of his tenure at Karluk, regularly collecting or measuring water temperature profiles, plankton samples, transparencies, total residues, and several chemicals (pH, dissolved oxygen, carbon dioxide, phosphorus, silica, and nitrite nitrogen). During 1935–37 he focused his attention on water chemistry and concluded that phosphorus and silica might limit the lake's primary production, which affected the growth and survival of juvenile sockeye. He published the water temperature and chemistry data for 1935–36 (Barnaby, 1944), but most of the limnological data gathered during 1931–38 went unpublished.

Whenever Barnaby visited Karluk Lake in the 1930s, he regularly collected juvenile sockeye from the littoral zone with beach seines and gill nets to learn about their seasonal habitats, distribution, and growth. He measured the size of many young fish and examined their food habits, but most of this data remained unpublished except for that contained in his thesis (Barnaby, 1932). To learn more about juvenile sockeye in 1931, he tried to mark 25,000 sockeye fry at Karluk Lake, but he soon abandoned the idea after clipping the fins of several thousand fish and witnessing their high mortality.

Tom Barnaby with U.S. Bureau of Fisheries boat *Nerka,* Karluk Lake, ca. 1937. (Joseph Thomas Barnaby, from Lynn L. Gabriel, Herndon, VA)

Continuing in the tradition of all previous biologists at Karluk, in the 1930s Barnaby periodically surveyed the spawning sockeye at the lake and estimated the numbers using the lateral and terminal streams, lake beaches, and upper Karluk River. When spawners were abundant, he improved the survey's accuracy by using a standard counting method, rather than just guessing at the numbers. Although his stream surveys were never published, after several years of doing this work he understood that sockeye salmon used the various spawning habitats in a distinct seasonal pattern; these repeatable annual behaviors suggested the existence of subpopulations. Without a doubt, his stream surveys from this period are valuable historic records of how sockeye salmon used specific spawning habitats. In fact, Barnaby pursued these surveys even further and investigated the physical aspects of the different spawning habitats, including the dimensions and water flows of lake tributaries. He found that some small lateral creeks occasionally had such low flows that adult sockeye were excluded from using them. For example, he often checked the flow of Little Lagoon Creek and several times dug a deeper channel to let adult sockeye freely move to and from the creek's pools. In 1935 he twice measured the discharge of the upper Karluk River—15.2 m^3/second on 30 June and 7.2 m^3/ second on 15 August. He monitored the water level of Karluk Lake each field season and found that it fluctuated 38–76 cm. In 1936 he installed a rain gauge on Camp Island and diligently recorded the daily accrual.

Prior to Barnaby's years at Karluk, the charr-sockeye interaction remained largely uninvestigated, though most biologists believed that charr predation on eggs and juveniles reduced sockeye salmon abundance. All charr in the Karluk system were then thought to be one species (called "Dolly Varden"). To explore this subject further, Barnaby initiated several studies of charr in the 1930s; in particular, he investigated their food habits and migratory behaviors. Charr were abundant at Karluk in the 1930s, and Barnaby saw large masses of these fish during their spring–summer river migrations, especially the thousands that accumulated at the weir on the lower river. Initially during 1930–34, he examined a few charr stomachs from scattered locations around the Karluk system whenever the opportunity arose, but as the study developed (1935–37), he specifically sought out charr and inspected larger numbers. Surprisingly, he found little evidence that charr preyed on juvenile sockeye, but they certainly ate many eggs once sockeye adults began spawning. The charr residing in Karluk Lake fed

heavily on sticklebacks, stickleback eggs, and insect larvae in early summer.

Barnaby expanded his charr studies in 1937–38 to try to understand their migrations, tagging thousands of fish at the lake and lower river and then searching for marked fish with his USBF assistant, Allan DeLacy. It soon became clear that two charr populations inhabited the Karluk system, one that migrated annually between the lake and ocean and another that remained year-round in the lake. In addition, he gathered data on the growth rates of the two charr populations and documented the amount of straying in the migratory population between different river systems of Kodiak Island. Unfortunately, Barnaby never published his charr studies, except for brief reviews (Higgins, 1938, 1939). When Barnaby left the Karluk research program in July 1938, he gave all of the charr data to DeLacy, who used them in his Ph.D. dissertation (DeLacy, 1941).

During Barnaby's nine years at Karluk, access to the lake was nearly the same as for all previous biologists. Supplies, research gear, and building materials delivered to Larsen Bay cannery by USBF patrol vessels, cannery boats, or chartered ships were transported by USBF dory to Dreadnaught City, the cabins and storage sheds located 6.5 km west of the cannery. Items that were larger or heavier than normal were delivered by USBF vessels to Dreadnaught City. The Fordson tractor and sled were used to haul supplies across the portage trail to the cabin and small boathouse on the river, but at times when the tractor was inoperable, everything was backpacked to the river. Often, one night was spent at the Portage cabin in order to get a fresh start for the lake the next morning. The 14 km trip by small skiff from the Portage to the lake took 7–9 hours depending upon the size of the load, river conditions, weather, and intensity of biting insects. The outboard motor was

Tom Barnaby hauling boat with Fordson tractor and sled, Karluk portage trail, 1936. (Joseph Thomas Barnaby, from Lynn L. Gabriel, Herndon, VA)

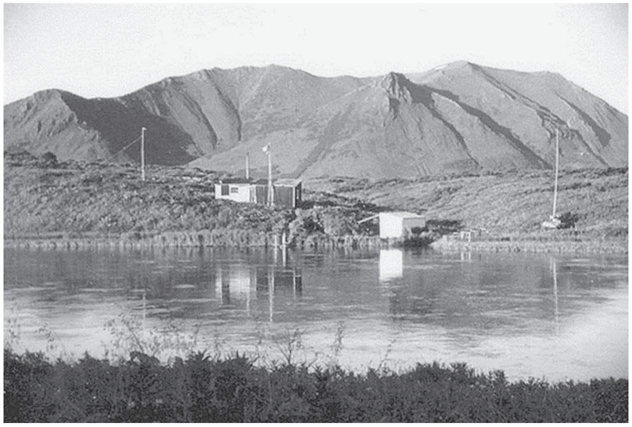
Pulling skiff up the Karluk River to Karluk Lake, 1942. (Allan C. DeLacy, from Catherine J. DeLacy, Seattle, WA)

useful for only the first part of the deep slow river, but once shallow water was reached, the boat was pulled and pushed upstream. Sometimes supplies were temporarily cached on the riverbank to lighten the load. At Karluk Lake, it took another hour to travel 10 km by boat between the outlet and Camp Island cabin.

During this era, the task of hauling supplies to Karluk Lake from Larsen Bay often consumed more than a full day under the best conditions, and often extra time was needed to fix mechanical problems of the tractor or outboard motors. Obviously with these rustic conditions, an important prerequisite for a field biologist was the ability to maintain and repair equipment. Retracing the route, the trip downriver from the lake to the Portage typically lasted 3–5 hours. Upon reaching Dreadnaught City, travel to the Larsen Bay cannery was done by dory or by walking 8.5 km along the beach.

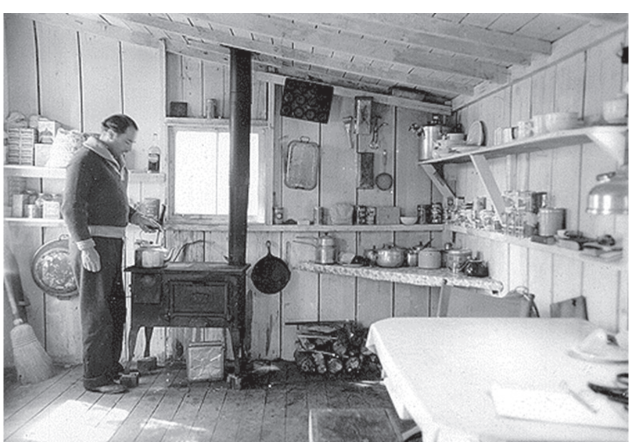
Because of his many ongoing studies in 1930–1938, Barnaby frequently traveled between five locations in the Karluk region: Karluk Lake, Karluk River weir, Larsen Bay cannery, Uyak canneries, and Karluk Spit. To reach the weir from Karluk Lake, he retraced his route to Dreadnaught City and Larsen Bay cannery, traveled 47 km around the island on a large boat to Karluk Spit, and motored by skiff up the lagoon to the weir. Between the canneries and Karluk Spit, he usually caught rides on USBF patrol vessels, cannery tenders, and fishing boats, only rarely attempting the trip in a USBF dory. When the ocean route was too rough to land at Karluk Spit, he instead floated downriver to the weir.

During Barnaby's nine field seasons at Karluk, he only saw airplanes overhead four times and only once flew from Kodiak to Karluk Lake with USBF officials in 1936. Undoubtedly, this was a chartered flight since



U.S. Fish and Wildlife Service cabin and boathouse, Karluk River Portage, 1944. (Jerrold M. Olson, Auke Bay, AK)

U.S. Bureau of Fisheries Camp Island cabin and boathouse, Karluk Lake, 1930s. (Joseph Thomas Barnaby, from Lynn L. Gabriel, Herndon, VA)



Tom Barnaby in Camp Island cabin, Karluk Lake, 1930s. (Joseph Thomas Barnaby, from Lynn L. Gabriel, Herndon, VA)

USBF aerial patrols were not yet common around Kodiak Island, though they were just beginning to be used in other areas of Alaska (Bower, 1937). To reach Alaska and Karluk at the start of each field season during 1930–1938, Barnaby traveled north from Seattle or San Francisco on USBF patrol vessels or APA and commercial steamships.

The USBF cabins at Dreadnaught City, the Portage, and Camp Island were important facilities for Barnaby's research, giving shelter, laboratory space, and storage along the main travel and supply route. He constantly maintained and improved the cabins, added shelves, painted, re-roofed with corrugated metal, patched windows, and repaired leaks. At Camp Island, he added an interior partition and porch to the cabin and built a boathouse and supply cache for winter storage. The lumber and building materials for these projects were arduously hauled by boat up the river.

In contrast with previous field biologists, Barnaby had reliable radios that allowed him direct communication between Karluk Lake, Larsen Bay, and Karluk Spit. When at the lake, he regularly checked on the current escapement figures, directed the work of assistants stationed at the weir or canneries, learned about the arrival dates of USBF patrol vessels and officials, and followed the progress of the commercial salmon fishing season. At Camp Island, he usually planted a garden each year to add fresh vegetables to his diet. With the considerable time Barnaby spent at Karluk each year, it is perhaps not surprising that he occasionally felt earthquakes and experienced ash falls from the volcanoes on the Alaska Peninsula across Shelikof Strait.

Although Barnaby primarily visited Karluk Lake to study its sockeye salmon and collect limnological samples, he was intensely curious about many other species and phenomena, and his notebooks are filled with observations about the region's plants, birds, and bears.[55] For example, he noted the seasonal change in Karluk's landscape—from the brown hills when he arrived each spring, to the slight greening a few weeks later, to the lush green of summer, and to the reds and browns of autumn. The spring growth of "nettle" and "bamboo grass" drew his attention, as did the seasonal succession of different flowers and later development of berries.

Karluk's birdlife was particularly captivating, and he compiled a detailed list of bird species for the re-

[55] J. Thomas Barnaby 1930–37 notebooks. Located at NARA, Anchorage, AK.

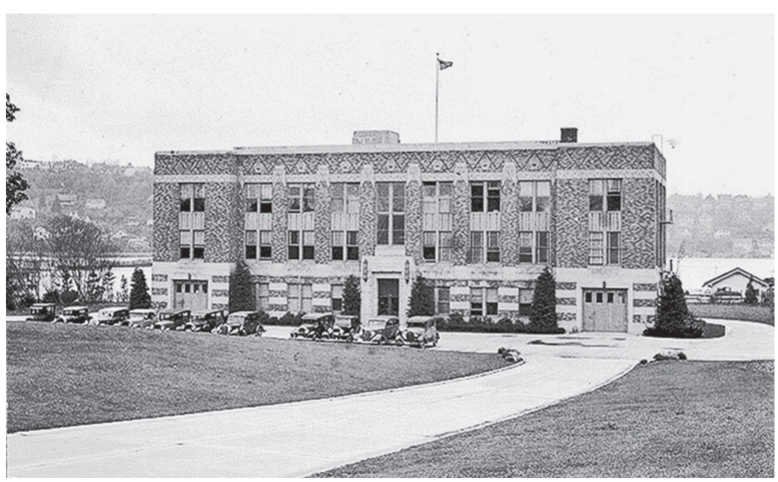
Barnaby Ridge, Karluk River near Portage, ca. 1935. (Joseph Thomas Barnaby, courtesy of Lynn L. Gabriel, Herndon, VA)

gion in 1937 and collected bird skins.[56] While living at Karluk Lake, he raised young seagulls, various waterfowl, and northern shrikes. Yet, his interest in Karluk's birdlife was not entirely observational, and it was common during this era for the field biologists to hunt waterfowl and ptarmigan to supplement their food supply. At Gull Island, the small isle next to Camp Island, biologists infrequently gathered seagull eggs for food, though Barnaby was more interested in recording the numbers of seagull nests, eggs, and young produced each field season. Karluk's brown bears also drew Barnaby's interest, and in 1936 he built a bear-viewing platform 8 m high in a large cottonwood tree at Halfway Creek. His broad interests in Karluk's wildlife were amply recorded with hundreds of photographs.[57]

Prior to 1932 no spruce trees or other conifers existed in the natural vegetation of the Karluk region or southwestern Kodiak Island because these trees had not yet reinvaded the area after the island's glaciers retreated thousands of years ago. Spruce trees had reinvaded and formed thick forests on Afognak Island and northeastern Kodiak Island, but the natural dispersal of these trees southward proceeded slowly, leaving most of southern Kodiak Island clothed with sweeping green vistas of grasses, herbs, shrubs, and occasional groves of cottonwood trees. As a curious sidelight to Barnaby's years at Karluk, in 1932 he transplanted several young spruce trees to Camp Island, first digging them up in Kodiak on 13 July 1932 and then planting them at the island cabin on 22 July. The transplants looked rather sickly the first year, but some survived and grew. Over the next few years, he cared for the spruce trees and occasionally moved them to better sites on Camp Island. The spruce trees reached heights of about 1.5 m in 1944, 1.8 m in 1948, 2.4 m in the 1950s, and much larger in the 1960s. In 1936 he planted a small

[56] The 1937 bird list is recorded in his notebook for that year (See footnote 55). It is unknown if the bird skins were placed in a museum collection.

[57] Barnaby took hundreds of photographs during 1930–38 of the Karluk landscape, his research activities, sockeye salmon, Karluk River weir, boats, flora and fauna, canneries, biological assistants, and people he met. His photographs included black-and-white stills and movies; many of these were developed in a darkroom at Larsen Bay cannery. Some of Barnaby's still photographs of Karluk from the 1930s have been discovered in his personal collection and at NARA, Anchorage, AK, but the location of his movies remains unknown. The ultimate disposition of Barnaby's photographs following his death in 1998 is unknown, but these likely were retained by his great niece Lynn Gabriel.



U.S. Bureau of Fisheries, Montlake Biological Laboratory, Seattle, Washington, ca. 1933. (Joseph Thomas Barnaby, courtesy of Lynn L. Gabriel, Herndon, VA)

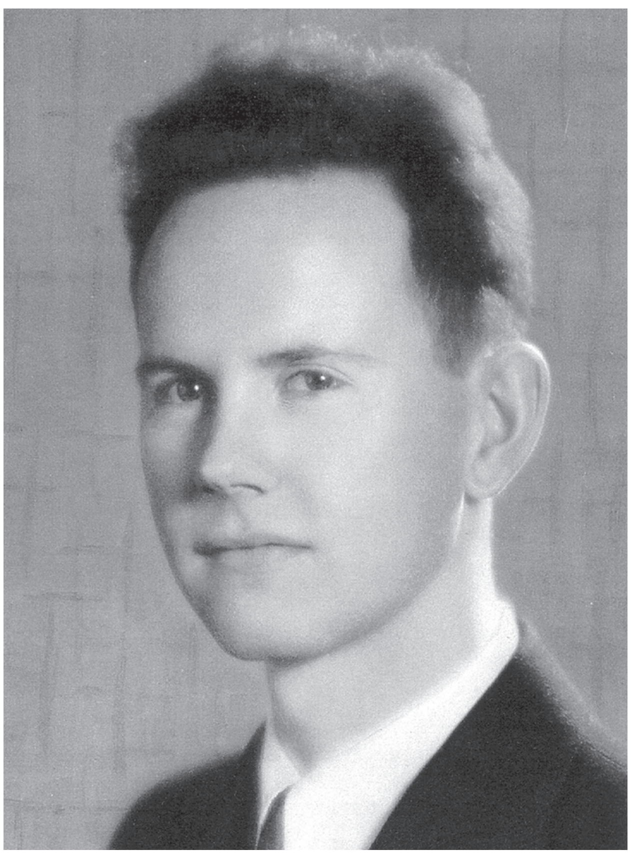
spruce tree on each side of the lake's outlet, but their fate remains unknown.

During Barnaby's tenure as Karluk's research leader, the USBF built the Montlake Laboratory in Seattle, Washington, in 1931. This biological laboratory served as the official federal headquarters of the Karluk sockeye salmon studies for the next 25 years, until those programs were transferred to Juneau, Alaska in 1956.

Allan C. DeLacy

1937–42

Allan Clark DeLacy was hired as a Junior Aquatic Biologist in 1936 by the USBF Montlake Biological Laboratory in Seattle. He first assisted Barnaby at Karluk for 1.5 years and then led these studies for the next 4.5 years until 1942. DeLacy had recently earned his B.S. (1932) and M.S. (1933) degrees at the School of Fisheries, University of Washington. He was placed in charge of the USBF's Karluk studies in July 1938 after Barnaby transferred to the salmon research program at Bristol Bay. During DeLacy's tenure at Karluk, he completed his Ph.D. at the University of Washington in 1941; his dissertation was on Karluk's Dolly Varden and Arctic charr. His fisheries work at Karluk comprised three main topics: Dolly Varden and Arctic charr studies, search for evidence of sockeye salmon subpopulations, and collection of run composition data on sockeye salmon. In 1940, during DeLacy's years at Karluk, the USBF and Bureau of Biological Survey were merged as the U.S. Fish and Wildlife Service (FWS).



Allan Clark DeLacy (1912–1989). (Allan C. DeLacy, from Catherine J. DeLacy, Seattle, WA)

Following on and expanding Barnaby's previous work, DeLacy intensively studied Karluk's two charr species, the Dolly Varden and Arctic charr. His research topics included charr taxonomy, migrations, food habits, and life histories. To capture charr from the full range of habitats in the Karluk ecosystem, he used the Karluk River weir, a temporary weir and trap on the Lower Thumb River, beach seines, gill nets, and a large fyke net that could be fished at any lake depth. To confirm that Karluk's Dolly Varden and Arctic charr were distinct species, DeLacy and Morton (1943) examined numerous anatomical characters of many specimens in 1939–41. DeLacy tagged more than 28,000 charr in 1937–40 and recovered about 4,500 of these through 1942. His results showed that Dolly Varden annually migrated between Karluk Lake and the ocean, while Arctic charr remained in the lake (DeLacy. 1941). Surprisingly, a few of his tagged charr continued to be recovered by biologists until 1949, many years after he had left the Karluk research program. While doing the tagging work, DeLacy also collected data on the age, spawning condition, and size (length and weight) of charr. Since charr scales were too small to age and otoliths (small ear stones that often have visible annual marks) seemed unreadable, he finally used length-frequency diagrams to determine the fish's age. By comparing the size differences of charr between tagging and recovery dates, he was able to calculate their growth rates.

During DeLacy's early years at Karluk, charr continued to be widely condemned in Alaska as serious predators of juvenile sockeye salmon. Barnaby began to examine this assumption in 1935–36, but DeLacy and his assistant, William Morton, wanted to resolve this question. Accordingly, they undertook a comprehensive study of charr food habits during 1939–41. To do this, they examined the gut contents of more than 5,000 charr at Karluk, but unexpectedly, less than 1% contained juvenile sockeye salmon (DeLacy, 1941; Morton, 1982). From this data, DeLacy concluded that Karluk's charr were not serious predators of juvenile sockeye, and instead, suggested that charr may benefit

juvenile sockeye by controlling the abundant stickleback competitors. DeLacy also briefly checked the food habits of 20 mergansers *Mergus* sp., and one kittiwake, *Rissa* sp., at Karluk in 1942 and found that most had eaten sticklebacks. Only one merganser contained juvenile salmonids, most likely coho salmon.

Although DeLacy is best known for his charr studies at Karluk, perhaps equally important, but largely unknown to other biologists, was his major study of its sockeye salmon subpopulations during 1939–42 (he used the term "races"). Previous biologists had suggested that Karluk's sockeye salmon had different subpopulations, the most obvious being the spring and fall runs. But DeLacy was the first to examine this question by measuring the anatomical characters of thousands of adults from many Karluk locations. When he first examined adult sockeye taken from the ocean or Karluk Lagoon in 1939–40, he found little evidence of subpopulations. Yet in 1941–42 when he examined adult sockeye from different spawning habitats at Karluk Lake, distinct subpopulation differences were evident:

> [Morton commenting on sockeye subpopulation study at Karluk Lake with DeLacy, 11 July 1941] Worked over statistical data on red salmon with Al after supper—he's found a significant difference between Lake & creek spawners in g.r. [gill raker] & vert [vertebrae] count—as we figured we would.
>
> [Morton's summary of a radio message from DeLacy, 27 July 1941] Find significant statis[tical] diff[erence] between g.r. [gill raker] & vert [vertebrae] count of Moraine Cr. & Lower Thumb Reds. . . .[58]

Because his 1941 results supported the subpopulation idea, DeLacy began tagging adult sockeye at the weir in 1942 and then searched for recoveries on the spawning grounds. This work demonstrated the segregation of different sockeye subpopulations to specific spawning habitats at Karluk Lake:

> [Concerning subpopulations of Karluk's adult sockeye] The analysis of morphomentric data from salmon taken at the mouth of the Karluk River in 1939 and 1940 has revealed no consistent differences between individuals of the early and late runs. However, the analysis of like data from fish taken on various spawning areas within the river system has indicated that such areas are frequented by racially distinct populations. The investigation of this problem is being continued by further collection of morphometric data and by a tagging program, which is being expanded in the present season.
>
> As in 1941 statistically significant differences have again been found to exist between the populations which occupy certain of the spawning grounds from which samples were taken. No differences of statistical significance have been discovered between either vertebral or gill raker counts from samples collected in 1941 and in 1942 at the same place and at the same time of year. It has become evident that even in the relatively small Karluk watershed the segregation of the maturing salmon after they enter the lake and move onto the various spawning grounds is not the result of a random dispersion. The racial studies being conducted at Karluk Lake offer further confirmation of the parent–stream theory and indicate that mature salmon may return to the very tributary in which they originated even though other suitable spawning areas are nearby.[59]

As a dramatic example, DeLacy watched adult sockeye migrating up the O'Malley River, at the head of Karluk Lake, segregate into one group that entered Canyon Creek and another group that continued up the main river. Unfortunately, he never published his 4-year study of Karluk's sockeye subpopulations, this omission causing later biologists to unknowingly repeat much of his work. Such a publication in the early 1940s would have been a remarkable advancement of knowledge about Karluk's sockeye salmon. And yet, considering the tumultuous world events of the early 1940s, DeLacy's lapse of publication is perhaps understandable.

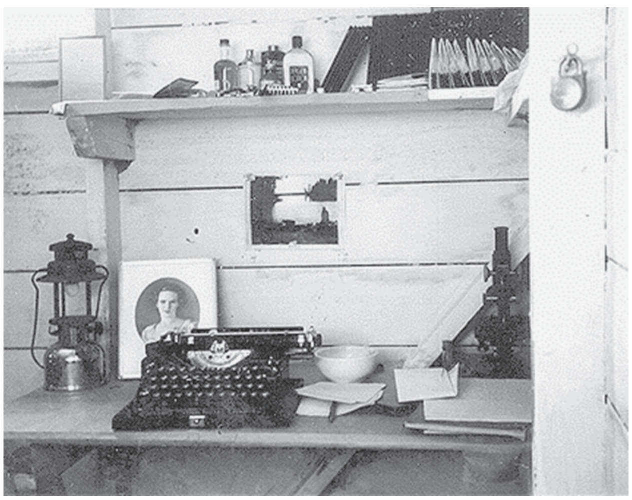
In conjunction with his subpopulation studies, DeLacy was the first Karluk biologist to experimentally test the fidelity of sockeye salmon in returning to their natal spawning site. In 1942 he collected and tagged adult sockeye at Thumb River beach and then transported and released them at other Karluk Lake locations. Most of these fish soon returned to the original beach; clearly adult sockeye salmon were not easily deterred from their natal spawning site.[60] Although his study was not fully appreciated at the time, this extraordinary result gave strong evidence of sockeye subpopulations and the home stream theory.

[58] William M. Morton 1939–41 notebooks. Original notebooks in personal papers of Robert S. Morton, Portland, OR.

[59] FWS Annual Report of Fisheries Research, 1941 and FWS Monthly Report, October 1942. Located at NARA, Anchorage, AK.

[60] DeLacy photographed these seining and tagging activities at Thumb River beach. While DeLacy most likely conducted this tagging experiment, no author was given on the unpublished handwritten report. FWS. 1942. Salmon tagging experiments at Karluk Lake – 1942. Located at NARA, Anchorage, AK.

Installing the Karluk River weir, Portage, 1942. (Allan C. DeLacy, from Catherine J. DeLacy, Seattle, WA)



Biologist's desk at field camp, Karluk, 1941. (Allan C. DeLacy, from Catherine J. DeLacy, Seattle, WA)

By the 1930s and 1940s, part of the Karluk research program was now a routine continuation of studies and tasks begun by previous biologists. Of course, the weir was installed and operated each year with at least some assistance from the research biologists, and run composition data (age, size, and sex) were regularly collected from sockeye smolts and adults. DeLacy installed the Karluk River weir each spring and occasionally helped count salmon, but the weir crew did most of the routine work. He was largely responsible for relocating the weir from the lower river to the Portage, transporting the lumber there in 1941 and installing it in 1942. Sockeye smolts were not marked during DeLacy's years at Karluk, but he continued the ocean survival studies of Rich and Barnaby and spent much of the field season during 1937–39 looking for previously marked adults at nearby canneries. It is unclear why, despite his diligent efforts, these data on marked adults and ocean survival were never used or published. DeLacy routinely collected limnological data at Karluk Lake during 1937–42, yet interest in this topic had waned and none were ever published.[61]

DeLacy and his assistants collected fecundity data from over 500 adult sockeye at Karluk during 1938–41, the first time such data had been gathered since Rich made his small collection in 1926. DeLacy's data were valuable since egg counts were made from all parts of the migration season. Fecundity increased with the season, and more eggs occurred in the left ovary than in the right ovary:

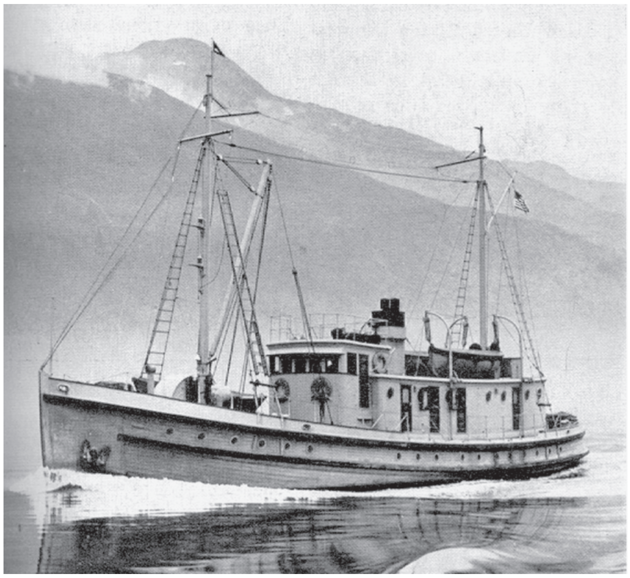
> [Fecundity of Karluk's sockeye salmon, 1940] The fecundity of Karluk red salmon was studied during 1940 by the collection of approximately 10 egg samples per week during the period from June 1 to September 13. Only salmon 60 centimeters in length were used in the experiment. It has been found that the number of eggs per female increased as the season progressed. The average number of eggs per fish was 2955 in June and 3643 in September . . . No explanation of this phenomenon was suggested by an age analysis of the fish . . . Each week during the season the average number of eggs in the left ovary was greater than the number in the right ovary.[62]

DeLacy's fecundity data were later analyzed and published by Rounsefell (1957).[63]

[61] The raw limnological data from Karluk Lake for 1937–42 are located at NARA, Anchorage, AK.

[62] FWS Monthly Report, December 1940. Located at NARA, Anchorage, AK.

[63] Additional egg fecundity data occurs in the records of the sockeye salmon hatchery operated on Karluk Lagoon in 1896–1916. APA. 1906–16. Karluk hatchery yearly reports. Located at NARA, Anchorage, AK.



U.S. Bureau of Fisheries patrol vessel *Crane,* Alaska. (H. C. Scudder, from Thompson, 1957)

During DeLacy's six field seasons at Karluk (1937–42), he divided his time between Karluk Lake, Karluk River weir, and the Larsen Bay and Uyak canneries. At the lake, the USBF cabin on Camp Island served as the research base. This site also had a boathouse and at least two small boats with outboard motors for travel around the lake. Getting to and from the lake typically required a boat trip on the river, often with a stopover at the Portage or Dreadnaught City cabins. DeLacy's assistant, Clarke M. Gilbert, established a new overland trail between Park's Cannery on Uyak Bay and Karluk Lake in 1940. This route followed several creeks and valleys from Uyak Bay and ended at the mouth of Lower Thumb River on Karluk Lake. FWS biologists regularly used Gilbert's trail in 1940–41. As an interesting sidelight to these years, President Theodore Roosevelt's son, Kermit, visited DeLacy at Larsen Bay cannery in 1937 or 1938, and then again at Karluk Lake, where Kermit hunted its brown bears. It was also during DeLacy's time at Karluk that President Franklin D. Roosevelt issued Executive Order 8857 that established the Kodiak National Wildlife Refuge on 19 August 1941. The refuge's main purpose was to preserve a large tract of natural habitat for the island's brown bears; the protected area included all of Karluk Lake and most of the Karluk River.

Each field season DeLacy traveled between Seattle and Kodiak Island on a USBF or FWS vessel (*Crane, Eider,* or *Penguin*) or on commercial passenger steamers. Movements of these vessels came under tight military control during the war years, especially after Attu and Kiska islands in the western Aleutian Islands were captured by Japan in 1942. To prevent enemy detection, the vessels were darkened at night, and travel schedules were kept secret, even from close family members. During the war years, DeLacy and his assistants occasionally spotted military aircraft over Karluk Lake, but they received no support from USBF or FWS airplanes. In the evenings, they anxiously listened to their radios for the latest war news.

William M. Morton

1939–41

William Markham Morton worked at Karluk during 1939–41 as a USBF and FWS biological assistant to DeLacy. Since many of the Karluk studies then were jointly conducted, it is difficult to separate the field activities of Morton and DeLacy. For example, both biologists tagged and recovered charr, examined charr food habits, investigated sockeye salmon subpopulations, and installed the Karluk River weir each year. Yet, Morton conducted several independent studies at Karluk

William Markham Morton (1905–1981). (From 1981 *Fisheries* 6(2):32, courtesy of the American Fisheries Society)

and took the lead in some joint studies. Because of his wide-ranging biological interests and many accomplishments, Morton was obviously more than a field assistant to DeLacy. In particular, Morton focused his Karluk research on three topics about Dolly Varden and Arctic charr: their taxonomic differences, their food habits, and their external and internal parasites.

Morton claimed that the greatest discovery of his entire fisheries career was when he found that two distinct charr species inhabited the Karluk ecosystem—Dolly Varden and Arctic charr. He did this during his first field season at Karluk, the holiday of 4 July 1939 being momentous (Morton, 1975). Prior biologists believed that only one charr species, the Dolly Varden, was present at Karluk, though Barnaby's tagging work in 1937–38 distinguished migratory and nonmigratory races (Higgins, 1939).

Morton made his discovery by closely examining the anatomical characteristics, color patterns, and associated parasites of charr (then called "trout"). He first worked with DeLacy at the Karluk River weir in May–June 1939, examining, measuring, and tagging thousands of Dolly Varden as they migrated downstream to the ocean. In late June the biologists went to Karluk Lake to collect charr from the lake, its tributary streams, and the upper river. Almost immediately, Morton noticed differences between the charr at the lake and those at the lower river, and he suspected they may be different species:

> [Karluk Lake, 24 June 1939] Then we loaded up the seine & went across the lake to Half-way Creek & took two hauls for trout—got 52—5 with tags—brot them back to Camp. Al weighed & measured them & I examined their stoms [stomachs]. Such a difference inside & out from the sea-going fish at the weir—hardly know them as the same fish.
>
> [Karluk Lake, 4 July 1939] Altho we were going to do a bit of cannonading with our rifle to celebrate the birth of our nation, we didn't get around to it. I was all excited over something else anyway. I have been strongly suspicious of a set of standard differentiations between the red or lake type Dolly Varden & the green or sea-going type—so I have been spending considerable time on the side making a series of measurements & observations on the red type. Last night when we came in we had 5 green & 5 red types with belly tags. I could hardly wait to look at the green ones—but like a small boy at Xmas eve—I waited with patience until morning—including my hopes in my nightly prayers—so I was up at 6 AM this morning and made breakfast—flapjacks & cereal—cocoa—fruit—& as soon as we did the dishes I set up my lab here in the kitchen. Imagine my gleeful thrill to find several distinct differences in structure esp. in no. of gill rakers on the first gill arch & the total no. of vertebrae—there is a possibility of two distinct species here—which problem I intend to pounce on with all I have! I must examine 500 or 1000 of each from different parts of the lake before making a definite statement on the matter—but I sure got a big kick out of realizing that there is a strong possibility it is staring me right in the face. Al thinks so too—so we are going right after it . . . But I won't forget this safe & sane fourth I don't believe—plenty "bang" in it for me today! Oh! If I only am on the rite road! I'd give my life for it.[64]

To pursue the species question, Morton began gathering morphological and meristic data on charr collected from many aquatic habitats at Karluk. He prepared color drawings and made cast models of the two types. His preliminary data supported the existence of two species, with the possibly of even a third species in some small creeks. He referred to these as the "ocean" or "green" charr for the migratory type (Dolly Varden), the "lake" or "red" charr for the nonmigratory type (Arctic charr), and the "creek" charr for those inhabiting small streams above impassable waterfalls.

Morton's early ideas on charr taxonomy were soon challenged by the noted fish biologist Carl L. Hubbs, who by chance visited the Karluk River weir in August 1939 while conducting a special investigation of USBF operations in Alaska. During the 1-day visit, Morton anxiously presented Hubbs with the recently collected charr data that supposedly distinguished the two species:

> [Karluk River weir, 4 August 1939] Arrived at spit just at 8 & in a few minutes saw *Brant* steam up from behind the Head . . . met Dr. Hubbs. He suggested we motor up to weir in their speedboat & we could talk on the way. So he asked me what I was working on & away we went. I made the fatal error of telling him we thot we had three species of *Salvelinus* here on Kodiak! He smiled & after listening to my descriptions expressed the opinion that they probably were races as in steelhead type & trout type of *gairdenerii.* I said yes I was afraid of that—he said "well—you needn't be afraid of that"—and I felt even more like kicking myself!
>
> I unfolded my sketches & gill raker & vertebrae counts & other charts & he studied them—didn't think much of the sketches—but was very interested in the data sheets—He finally said he was sure it was a racial development—that these ocean going forms developed a distinct race alrite that was similar to salmonoid forms—body shape & silver color etc proved it—while the lake fish being isolated developed another form—stocky & many colored rainbow type of lake environment—also the creek type might be just an offshoot . . . Suggested scale analysis. Says they determine age of brooks that way & also to count scales & check otoliths & pyloric caeca. He believed that extreme emaciation &

[64] See footnote 58 (24 June and 4 July 1939).

parasitization of ocean type would tend to develop into the lake type.

So we went up to the weir & looked at salmon & he took pictures of it. Afterwards he stopped at cabin to examine some of our specimens. And like the spectacular fool I am—I dragged out the only two specimens we have of upstream lake migrants & he asked if I had checked them—no—labelled them—no—well how did I know they were what they were—I blurped—check them yourself I'm sure of them & by Jove—he set me back on my fanny by counting only 19 g.r. [gill rakers] in the only green colored "lake type" we have seen all season in 40,000 trout! Mark—will you never learn to be careful—and a bit less undramatic! All he had to do was point out how nicely this specimen illustrated his theory & I was sunk—but since recovering I have salvaged a lot of spunk—maybe he's rite so I better—record more carefully & accurately after this & be more sure & take it slower. Oh! He's a great guy this Dr. Carl Hubbs of Mich. U. . . . He wants to know where & when & how they all spawn & would then breed true. I suggested lake weir & he seemed in accord with it.[65]

Following Hubbs's suggestion, Morton unsuccessfully tried to age Karluk's charr using their scales. Scale diameters were proportional to fish lengths, but all scales seemed to have 13–16 rings regardless of size, and the scales of larger charr had regenerated centers. The scales of charr, in contrast with most other salmonid species, lacked the distinct annuli that are used to determine age. When Morton examined charr otoliths, he saw distinct growth rings, but was uncertain just how these correlated with age. For comparison, he examined the scales and otoliths of a 360 mm Karluk rainbow trout and found that both body parts had four rings. In contrast, a 360 mm charr had 8–9 otolith rings and 13–16 scale rings. Evidently, Karluk's charr grew much slower than its rainbow trout.[66]

Morton continued to collect taxonomic data on charr during 1939–41 from Karluk Lake and River, lake tributaries, and ocean waters along Shelikof Strait. He caught these fish with a full range of sampling gear (seines, river weir traps, dip nets, hook-and-line, fyke nets, gill nets, and ocean traps). The analysis of these charr specimens included detailed measurements and counts of numerous body features—length, weight, dorsal and anal fin rays, gill rakers, vertebrae, pyloric caeca, branchiostegal rays, scales, otoliths, body color and spotting, liver and swim bladder color, skull bones, and eggs. This mass of data, along with life history information, was used to distinguish the two charr species in the Karluk ecosystem (DeLacy and Morton, 1943). Although some uncertainties still remained about the distinctness of the two charr types at Karluk, most biologists accepted DeLacy and Morton's conclusions, and after 1943 most biological studies at Karluk distinguished the two categories.

Prior to Morton's study, the taxonomy of Karluk's charr was not an official part of the FWS research program. Instead, this work reportedly originated from Morton's curiosity and spare time efforts:

[Karluk, 1939–1941] I began recording morphometric (body) measurements and meristic (scales, bones) counts before dissecting each fish for internal studies which included tabulation of food items found in the stomachs and any parasites found in the alimentary canal or other organs or tissues. This work was done in my spare time, after we had taken the lengths and weights and recorded all tag numbers or marks (fins clipped off in various combinations at an earlier period in their lives) for our official record. (Morton, 1975)

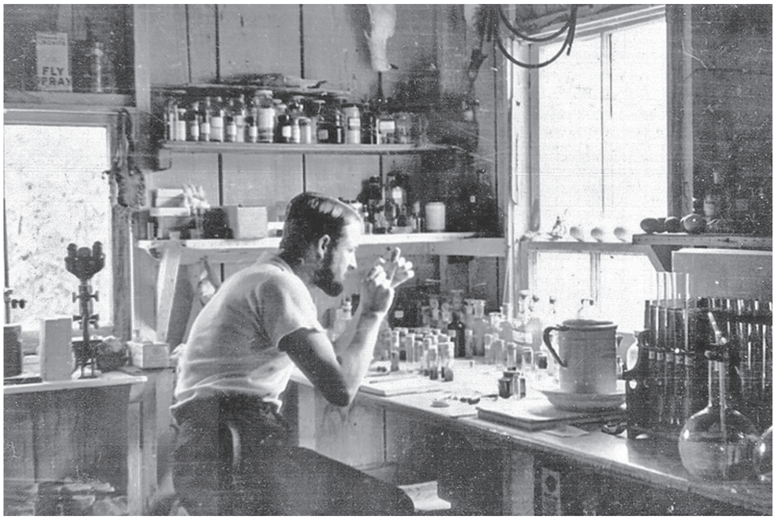
Further, it appears that Morton collected most of the anatomical data on the charr and was the main force pursuing this work, but DeLacy, being the senior FWS employee and having previous experience with fish taxonomy, took the lead in their joint publication (DeLacy and Morton, 1943). Morton highly respected DeLacy as a friend and competent biologist and viewed him as a role model. After working with DeLacy for just a few months in 1939, Morton declared that "in every way I've tested him, he's shaping more & more into a silent model for me to work on".[67] DeLacy, as leader of the Karluk research program, supported Morton's several independent studies.

A second major study that Morton pursued at Karluk was an investigation of charr food habits. During this era, thousands of Dolly Varden were annually destroyed at the Karluk River weir because it was commonly believed that charr predation decreased sockeye salmon populations. In 1939 Morton assisted DeLacy in his study of charr migrations and growth at Karluk, and it was a daily task to dispose of the charr caught at the weir, after first checking them for tags. The down-migrating charr caught at the weir in May–June were thin and emaciated, a glaring fact that seemed to contradict the belief that these fish heavily preyed on sockeye juveniles. Morton was curious to know if these charr had preyed on the sockeye smolts that also were abundant in the river. Thus, before discarding the captured charr, he examined their stomach contents, and, to his astonishment, found that most were empty. Since this direct evidence differed

[65] See footnote 58 (4 August 1939).

[66] See footnote 58 (26 August 1939).

[67] See footnote 58 (8 August 1939).



William Morton studying charr parasites, Camp Island cabin, Karluk Lake, 1940. (William M. Morton, from Robert S. Morton, Portland, OR)

so dramatically from prevailing attitudes about charr predation, Morton began a detailed study of their food habits. To add validity to the study, he examined charr from a wide range of seasons, habitats, and fish sizes. Surprisingly, after checking more than 5,000 charr at Karluk over three years, he found little evidence of predation on juvenile sockeye (Morton, 1982). In contrast, he found that charr ate many sockeye salmon eggs at the Karluk Lake spawning grounds, but believed this was a scavenging behavior, not predation. Soon thereafter, FWS Director Ira Gabrielson ended the Dolly Varden control program, in part because of Morton and DeLacy's results.

While Morton and DeLacy both participated in the charr food studies at Karluk (and benefited from Barnaby's previous work), apparently Morton was mainly responsible for this effort (Morton. 1975, 1982). His field notebooks document that he spent an enormous amount of time examining charr stomachs.[68] Yet, despite the major implications for how biologists should now view the charr-sockeye interaction at Karluk, and potentially for other Alaska regions, their complete study was not formally published for many years. DeLacy (1941) used the 1935–40 food habits data in his Ph.D. dissertation and summarized the results in their charr taxonomy paper (DeLacy and Morton, 1943). Morton tried for 40 years to publish the full results of the food habits study and finally succeeded near the end of his life (Morton, 1982). Unfortunately, the study remained largely unknown to other fishery biologists during these 40 years, and this lapse caused others to partially duplicate this work. Potentially, if Morton's results had been published earlier, Rounsefell (1958) may not have recommended that predatory fishes be eliminated from Karluk Lake as a way to increase sockeye salmon abundance.

Morton's third major study at Karluk was his investigation of the internal and external parasites of Dolly Varden and Arctic charr, though again he claimed that this was a "spare time" project (Morton, 1942). Unlike the charr taxonomy and food habits work that were jointly done with DeLacy, the parasite studies were entirely Morton's. He pursued this research because of long-standing interests in parasitology, not because the USBF or FWS requested them. After graduating from the University of Iowa with an AB degree in 1933, Morton spent three summers during 1935–37 studying parasitology at the University of Minnesota with William A. Riley. Thus, as Morton dissected and measured numerous charr for the taxonomy and food studies, it was only natural for him to record whatever parasites he found.

Morton began investigating charr parasites in 1939, his first year at Karluk, but these were only tentative efforts compared with his intense studies of 1940–41. During this period he enrolled as a graduate student at the University of Washington and worked with James E. Lynch, an invertebrate zoologist and expert in microscopic techniques. Lynch soon became a mentor for Morton and helped him identify parasites and suggested preservation and staining methods. Nevertheless, under the rustic field conditions at Karluk, Morton found that it was a frustrating trial-and-error process to preserve and prepare the parasites on glass slides. Furthermore, he found it time-consuming to collect charr parasites since the process required close examination

[68] See footnote 58.

of all external surfaces and internal organs. For example, he scrutinized the general body surface, fins, gills, muscles, mouth interior, esophagus, stomach, intestines, integument, and various organs (heart, liver, pyloric caeca, gas bladder, gonads, and kidney).

In total during 1939–41, he examined 135 Dolly Varden and 212 Arctic charr for parasites and identified 16 species (plus some unidentified forms). These charr parasites came from five major invertebrate groups—trematodes, cestodes, nematodes, acanthocephalids, and copepods. Dolly Varden and Arctic charr shared some parasite species, but other parasites were unique to each charr species. Morton believed the differences were related to the separate life histories and food habits of each species. Arctic charr were more heavily parasitized than Dolly Varden, and older fish had more parasites than younger fish. Significantly, the results of the parasite study reinforced those of the taxonomic study—that two distinct charr species inhabited the Karluk ecosystem. Morton never formally published the charr parasite results, but used them for his M.S. thesis at the University of Washington in 1942. It is unfortunate his work remained unpublished since this subject became of great interest to parasitologists at the Arctic Health Research Center, Anchorage, when they studied tapeworm life cycles at Karluk Lake in the 1950s (Rausch, 1954; Hilliard, 1959b, 1960).

Besides his focus on charr, Morton collected parasites from an astonishing array of fishes, birds, and mammals whenever the opportunity arose at Karluk. For fishes, he collected parasites from threespine stickleback, steelhead and rainbow trout, coastrange sculpin, juvenile and adult sockeye salmon, pink salmon, Chinook salmon, coho salmon, and Irish Lord sculpins. For birds, he examined mergansers, bald eagles, glaucous-winged gulls, Bonaparte's gulls, kittiwakes, terns, magpies, owls, and various ducks. For mammals, he studied brown bears, meadow mice, and a seal. By examining a broad array of animals, he hoped to understand the full complexity of a parasite's life cycle, especially since different life stages of a parasite often infected different hosts. Stickleback parasites particularly interested him because they could be easily transferred to charr hosts via the food chain. In fact, he theorized that Arctic charr had higher infestation rates of some parasites than did Dolly Varden because of their heavier predation on sticklebacks. Although little of his non-charr parasite work was ever published or presented in informal reports, Morton obviously collected much more information on this subject than was included in his M.S. thesis (Morton, 1942).[69]

Morton spent considerable time investigating the parasites of Karluk's brown bears. Whenever hunters shot a bear, he examined the carcass for parasites, in particular looking for and finding tapeworms. Likewise, during travels around Karluk Lake, he often examined bear fecal piles for parasites and soon realized that bear foods varied seasonally, with elderberries being a major food in late summer. To better understand the tapeworm's life cycle, he sampled Karluk Lake's plankton and found the ceracaria life stage of this parasite.[70]

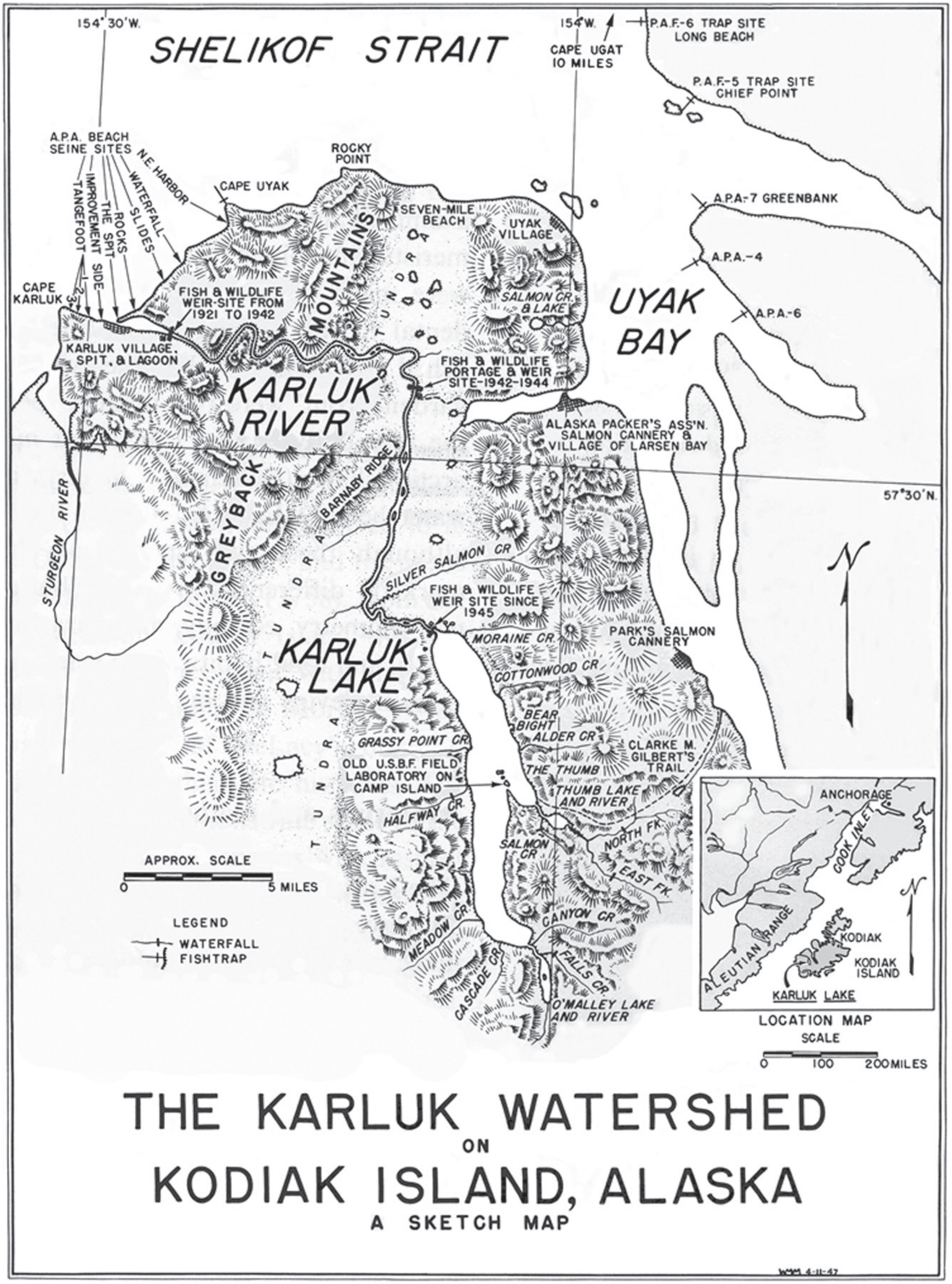
Besides his three main studies at Karluk, Morton was interested in many other biological topics and participated in other research efforts. His three notebooks from 1939–41 provide one of the most detailed, wide-ranging, accounts ever written about USBF and FWS field research at Karluk. They contain detailed chronicles of the seasonal changes in the region's aquatic and terrestrial biota.[71] Following is a brief list of Morton's other interests and activities at Karluk in 1939–41:

- Helped install and operate Karluk River weir, 1939 and 1941.
- Searched for marked sockeye salmon adults in the commercial catch at Larsen Bay cannery, these fish first being marked as smolts by Barnaby in 1935–36.
- Collected egg samples from sockeye salmon to determine their fecundity.
- Collected subpopulation data on sockeye salmon adults (length, number of gill rakers and vertebrae).
- Collected sockeye salmon smolts.
- Collected morphological and meristic data on other salmonids (Chinook, coho, and pink salmon and steelhead).
- Helped install and operate a weir and charr trap on the Lower Thumb River (1939–41) and at the Portage (1941).

[69] During the 1939–1941 field seasons at Karluk, Morton recorded his parasitological observations in a separate notebook and prepared numerous glass slides of collected specimens. We believe his parasite notebook and collection to be valuable Karluk resources, but their location is unknown, possibly having been donated to the University of Washington or some other institution.

[70] See footnote 58 (30 July 1941).

[71] See footnote 58. Each of Morton's field seasons at Karluk lasted about five months: 1939 (8 May–28 Sept.), 1940 (17 June–6 Oct.), and 1941 (12 May–24 September). Other biologists assisting Morton and DeLacy at Karluk during these years were Clarke M. Gilbert (1939–40) and Hal Plank (1941).



William Morton's 1947 sketch map of the Karluk watershed. (Modified from Morton, 1982)

- Helped tag and recapture charr.
- Described sockeye salmon spawning behavior and seasonal changes.
- Made colored drawings and casts of all Karluk fishes.
- Examined stomach contents of most Karluk fish species.
- Collected fishes for museum collections.
- Recorded birds seen in the Karluk area (seasonal changes, behavior, and nesting).
- Examined stomach contents of many Karluk birds and observed bird predation on juvenile sockeye.
- Collected bird skins and eggs for museum collections.
- Recorded seasonal development of the regional flora.
- Collected limnological data from Karluk Lake and its tributaries (water temperature, water chemistry, plankton, and benthos).
- Installed and maintained river thermograph and rain gauge; recorded water level changes of Karluk Lake; measured discharges of tributary streams.
- Mapped upper Karluk River.
- Photographed Karluk (black-and-white prints, color slides, 8mm movies).

It is likely that Morton's personal papers and collected specimens contain valuable and historic Karluk data, but their location remains unknown.[72]

In 1947 Morton prepared a detailed and informative sketch map of the Karluk River watershed. The map gave a clear depiction of the region's villages, canneries, landforms, ocean bays, rivers, and lakes, but it was valuable for showing the locations of six stationary fish traps and nine beach seine sites that existed in the 1940s. In addition, the map showed the three weir locations on the Karluk River and when each was used. For some streams at Karluk Lake, Morton marked where barrier waterfalls stopped the upstream migration of salmon.

Richard F. Shuman

1943–49

Richard F. Shuman, FWS fishery biologist, was placed in charge of the sockeye salmon studies at Karluk after DeLacy resigned in February 1943. Prior to this appointment, Shuman, a recent fisheries graduate of the University of Washington, had studied pink salmon for three years at the FWS Little Port Walter station in southeast Alaska. He led the Karluk studies for seven years (1943–49) and focused his research on six biological topics of sockeye salmon: migration travel time, run segregation to specific spawning sites, escapement-return relationship, bear predation, lake productivity, and fecundity.

Upon arriving at Karluk in the spring of 1943, Shuman first installed the Karluk River weir at the Portage and then worked to improve the portage trail between Larsen Bay and the Karluk River. Improvements were needed for easier transport of supplies across the unstable muskeg with the new FWS tractor (a Cletrac AG) and sled.[73] In July he explored Karluk Lake to survey the sockeye spawning habitats, and was impressed by the many brown bears that preyed on adult salmon. Although just a few months into his new job at Karluk, on this visit to the lake he searched for new sites for a weir and laboratory, wanting to consolidate both nearer the lake where most future research would occur. The Portage weir location, being far removed from the lake,

[72] We made preliminary efforts to locate Morton's specimens and research materials from Karluk. According to his son, Robert S. Morton, Portland, OR, for many years after 1941 his father maintained a research laboratory with specimens and unpublished material in his home basement (Robert S. Morton, personal commun. with Richard L. Bottorff, 1998). Apparently, most of this material was eventually donated to several institutions. In 1977, specimens and research data were donated to the School of Fisheries, University of Washington, in exchange for laboratory space and access to their collections. Whether the donated specimens included his entire collection of Karluk parasites, bird skins and eggs, and fishes is unknown, but at least a few Karluk fishes from De Lacy and Morton do exist in the University of Washington fish collection. Likewise, whether this donation included his raw data and unpublished notes from Karluk is unknown. In 1985, several years after Morton's death, his books were donated to the University of Alaska, Juneau, and an additional six boxes of research materials were donated to Glacier National Park, West Glacier, MT. The latter donation was primarily data and reports from Morton's research in the Flathead Valley, MT, but also included material from other areas. In 1998 Morton's six boxes of research materials remained in storage at Glacier National Park, and had not yet been inventoried (Leo F. Marnell, Glacier National Park, personal commun. with Richard L. Bottorff, 1998). Robert S. Morton retained his father's 1939–41 field notebooks, several colored drawings of Karluk fishes, a few black-and-white Karluk photographs, and three reels of 8mm movie film entitled "Karluk Village Fishing on Spit 1940" and "Karluk Lake and Weir with Peterson, Morton and Gilbert 1941".

[73] In 1943 Shuman shared this job with his two field assistants, Joseph Corkill and Joe Westaby.

Richard F. Shuman (1906–1954). (Richard F. Shuman, from Beryl Shuman, Minnetonka, MN)

made it inconvenient to operate the weir and also conduct biological studies at the lake. Clearly, his first visit to Karluk Lake formed long-lasting ideas that led to many of his future research projects.[74] Besides exploring the lake in 1943, Shuman collected fecundity data from nearly 200 sockeye salmon; Rounsefell (1957) later analyzed and published these data.

By mid August 1943 Shuman was increasingly occupied with operating and securing the Portage weir as decaying aquatic plants drifted downstream, accumulated on the upstream face, and threatened to washout the structure. The weir crew diligently cleaned away the plants for several weeks and kept the weir in service, but the ever increasing masses of plants finally overcame the crew's efforts and they had to dismantle the weir before the sockeye run ended and counting was complete for 1943. This frustrating experience reinforced Shuman's resolve to move the weir to a new site nearer to Karluk Lake, but it was not until September 1943 that he first realized the Portage site had a serious weed problem. By then, for logistical reasons alone, it was too late to change the 1944 weir location. Therefore, he again installed the 1944 weir at the Portage, but, as for 1943, it was rendered unusable late in the season, this time by a combination of decaying plants and pink salmon carcasses that drifted downstream. To prepare for 1945, Shuman and his crew spent most of the 1944 field season hauling materials, by brute force labor, to a new weir site near the lake. When at the lake they also surveyed the sockeye spawning habitats and examined charr stomachs for evidence of predation on juvenile sockeye.

In 1945 Shuman installed the Karluk River weir just below the lake's outlet and built a small cabin nearby for the weir crew and biologists. Because the new weir was now further removed from the commercial fishery, it was essential to know how long it took adult sockeye to reach the weir from the ocean. To measure this migration travel time, Shuman and his assistant, Philip Nelson, tagged thousands of spring- and fall-run sockeye at Karluk Lagoon in 1945 and 1946 and then recorded their passage at the weir (Gard, 1973). With these new travel-time results, commercial catches and escapements could now be better matched for calculating the seasonal variation of the total run and for managing the fishery.

Shuman and Nelson also used tagging methods to study the dispersion of adult sockeye to specific spawning sites at Karluk Lake during 1945–48. Their first indication that adult sockeye salmon might home to specific sites in and near the lake came in 1945–46 when the fish tagged in the travel-time study were later found on the spawning grounds. In 1947–48 they obtained even better records of this dispersion by tagging many sockeye at the weir and later finding them at specific spawning sites. Since the weir was then located near the lake, it was convenient for the crew to regularly survey the different spawning habitats for tagged fish throughout the entire run season. Some sockeye tagged at the weir in September 1948 were seen at spawning sites well into late October and November, including one observed at Thumb Lake under 8 cm of ice on 20 November.[75]

After several years of these tagging studies, Shuman and Nelson understood that sockeye salmon used the different spawning habitats at Karluk in a repeatable seasonal sequence each year. Spring-run sockeye spawned in lateral and terminal tributaries of Karluk Lake, while fall-run sockeye spawned in terminal

[74] Richard F. Shuman 1943–49 notebooks. Located at NARA, Anchorage, AK.

[75] Arthur Freeman 1948 notebook. Original notebook in personal papers of Arthur Freeman, Indianapolis, IN.

Richard Shuman with U.S. Fish and Wildlife Service boat *Nerka,* Karluk Lake, 1944. (Jerrold M. Olson, Auke Bay, AK)

streams, lake beaches, and the upper Karluk River. Of course, previous Karluk biologists had also observed this seasonal dispersion, but Shuman and Nelson were the first to accurately document the behavior. Yet, for unknown reasons, they never published their tagging results and later biologists repeated their work. Their tagging studies also showed that adult sockeye spent about one month in Karluk Lake before spawning, the same maturation period first discovered by Rutter and Spaulding in 1903.

In 1945 Shuman investigated the relationship between the escapements and returns of sockeye salmon at Karluk, possibly being inspired by Barnaby's 1944 paper on the topic. Barnaby analyzed escapement-return data for nine years (1921–29), while Shuman now had 19 years of data (1921–39). Shuman wanted to understand what escapement led to the greatest surplus of sockeye salmon at Karluk. In late 1945 he analyzed the data and prepared a manuscript for publication titled "Observations on escapements and returns of red salmon at the Karluk River," that recommended a relatively low escapement goal (350,000–500,000 per year).[76] Before publication, Shuman sent the manuscript in early 1946 to Willis Rich, who was then advising the FWS on its Pacific salmon studies. Rich argued that in setting an escapement goal it was insufficient to base it on the 1921–39 data alone, but should include information on sockeye abundance prior to 1921. He believed the data for 1921–39 failed to account for the true productive potential of Karluk's sockeye salmon because by that period the run was in a long-term decline. Rich believed that Karluk Lake's reduced fertility had caused the decline as fewer salmon-carcass nutrients supported the food base of juvenile sockeye. Instead, he argued for high escapements (2,000,000 per year) of sockeye salmon to Karluk Lake to restore its fertility.

Shuman and Rich exchanged ideas about Karluk's sockeye during 1946 and discussed ways to improve the manuscript (there was even brief mention of joint authorship). Eventually, Shuman accepted most of Rich's ideas and over the next few years he completely revised and expanded the manuscript and gave it a new title: "Biological studies of the red salmon *Oncorhynchus nerka* (Walbaum) of the Karluk River, Alaska: A report on the trends in abundance, with a discussion of the ecological factors involved."[77] He increased the escapement goals (350,000 spring run and 350,000 fall run) and recommended the fertilization of Karluk Lake to restore its nutrients. He also advocated an expanded research program on limnology, predation, stickleback competition, and marine migration studies. Finally in 1951 Shuman submitted his revised manuscript, "Trends in abundance of Karluk River red salmon with a discussion of ecological factors," for publication in the *Fishery Bulletin*.[78] His paper discussed a full range of subjects on Karluk's sockeye salmon; the table of contents included:

- Problems of conservation
- History of biological program
- Life history
- Composition of catch
- Returns from escapements
- Independence of spring and fall run
- Desired escapements
- Trends in abundance
- Factors affecting survival in fresh water
  - Topography and weather
  - Balance in nature
  - Civilization
  - Predators
  - Competitors
  - Food supply
- Effective escapements
- Spring and fall runs

[76] Shuman, Richard F. 1945. Observations on escapements and returns of red salmon at the Karluk River. FWS, Division of Fishery Biology. Unpubl. report. 17 p. Located at ABL, Auke Bay, AK.

[77] Shuman, Richard F. 1950. Biological studies of the red salmon *Oncorhynchus nerka* (Walbaum) of the Karluk River, Alaska. A report on the trends in abundance, with a discussion of the ecological factors involved. Unpubl. report. 73 p. Located at ABL, Auke Bay, AK.

[78] Shuman, Richard F. 1951. Trends in abundance of Karluk River red salmon with a discussion of ecological factors. Manuscript prepared for *Fishery Bulletin* 71, vol. 52. Unpubl. report. 56 p. Located at ABL, Auke Bay, AK.

Artificial fertilization of lake waters
Immediate steps proposed
Summary
Literature cited

In spite of Shuman's determined efforts to improve this manuscript, it was never published. The paper proceeded to the galley proof stage by late 1951, but then FWS officials stopped its publication. Though it is not clear why publication was canceled, and by whom, Shuman believed George Rounsefell was primarily responsible. Rounsefell, then Chief Editor and Reviewer of FWS publications, undoubtedly had seen Shuman's paper and had the authority to stop its publication, if desired. It is also likely that he knew Shuman was working on the Karluk manuscript well before 1951, and had seen earlier versions, since as Chief of the Branch of Anadromous Fishes he visited Shuman at Karluk Lake in 1947 to discuss the sockeye research program, which then was implementing some of Shuman and Rich's ideas:

> [Karluk Lake, 17 August 1947] Rounsefel, Kelez, Ball in about noon. Discussed plans with Rounsefel. Feeling so-so.[79]

But Rounsefell's involvement with the sockeye studies at Karluk was apparently much deeper in 1951 than a casual interest in the research program and its publications. Sometime in 1949–52, Lionel Walford, FWS Director of Research, assigned Rounsefell the job of analyzing the long-term set of data that had been collected on Karluk's sockeye salmon. Possibly, Rounsefell had already reached his own conclusions about Karluk's sockeye when he first read Shuman's 1951 manuscript, or had already started to write his own paper.

After working on his manuscript for over five years, Shuman gave up further efforts to revise the 1951 version after its publication was blocked. Nevertheless, in December 1952 Rounsefell sent Shuman a large 72-page manuscript entitled, "Population dynamics of the sockeye salmon, *Oncorhynchus nerka,* of Karluk River, Alaska," with Rounsefell as senior author and Shuman as junior author.[80] Joint authorship suggested that they had collaborated on the paper, but Shuman had, in fact, no knowledge of the paper until receiving the December 1952 copy. This new manuscript discussed subjects previously presented in Shuman's 1951 paper, but some conclusions and recommendations of the two manuscripts conflicted, such as the presence of subpopulations, the seasonal distribution of the runs, and how the fishery should be managed. Yet, many of Rounsefell's recommendations were similar to Shuman's, including the need for limnological studies and the possibility of fertilizing Karluk Lake to enhance its fertility.

Shuman forcefully told the FWS Regional Director that he did not want his name on Rounsefell's paper, believing that many conclusions were incorrect and possibly harmful to the run.[81] In particular, the two biologists sharply differed over whether the sockeye salmon run was a single population or had distinct components—Rounsefell declared the run was a single population, Shuman stated that spring and fall runs were independent. Shuman was also concerned about Rounsefell's recommendation to curtail spring and fall escapements in favor of larger mid-summer escapements. In response, Shuman prepared a detailed critique of Rounsefell's paper and recommended that it not be published. Of course, Shuman's response was undoubtedly affected by the unpleasant events that had stopped his 1951 paper. In any event, Rounsefell's 1952 manuscript was an early draft of the large paper he eventually published in 1958.

It was unfortunate that Shuman's 1951 paper went unpublished because it was a well-written statement of then current knowledge about Karluk's sockeye salmon and the actions needed to increase these runs. The paper had great legitimacy because Shuman's analysis was based on many years of firsthand field observations. He gave clear statements about the independence of spring- and fall-run sockeye and explained how the runs used different spawning habitats in the Karluk ecosystem. He provided a still relevant discussion of the factors that affect the freshwater survival of juvenile sockeye and forcefully argued that salmon-carcass nutrients influenced Karluk Lake's fertility and the production of sockeye salmon. Shuman discussed the possibility of fertilizing Karluk Lake to enhance its fertility and recommended detailed studies of the lake's limnology, juvenile sockeye, and sticklebacks. He emphasized the need to accurately measure the sockeye smolt out-migration and recommended changes to the 1924 White Act to allow constant, sustainable escapement goals for the Karluk system.

Of course, Shuman's interaction with Rich was partly responsible for the scope and content of his 1951

[79] See footnote 74.

[80] Rounsefell, George A., and Richard F. Shuman. 1952. Population dynamics of the sockeye salmon, *Oncorhynchus nerka,* of Karluk River, Alaska. FWS, Woods Hole, MA. Unpubl. report. 72 p. Located at ABL, Auke Bay, AK.

[81] Memo (7 January 1953) from R. F. Shuman, FWS, Juneau, to Regional Director, FWS, Juneau AK. Located at ABL, Auke Bay, AK.

unpublished paper. Discussions with Rich in 1946 had convinced Shuman of the need to study the lake's limnology, and, indeed, a full range of lake data were collected during 1947–49. Soon thereafter, Shuman and Nelson wanted to field test the lake fertilization idea and selected Bare Lake for the trial. Although Nelson was in charge of the Bare Lake experiment after Shuman left the Karluk studies, the lake fertilization idea began with Rich and Shuman.

Of Shuman's many studies at Karluk, he is perhaps best known for his research on brown bear predation of sockeye salmon. Ever since his first field season in 1943, Shuman was interested in the brown bears at Karluk Lake and the many adult sockeye these predators killed:

> [Salmon Creek, 10 July 1943] Bears *extremely* numerous on this branch. Saw 5 bear here, being charged by female with cubs. Outcome fortunate! Must observe extreme caution on all these streams in future . . . Loss of fish to bears apparently enormous, though no estimate in numbers possible. Remains of those killed by bear are everywhere.
>
> [Karluk Lake, 17 July 1943] Bears were *very* numerous over entire Upper Thumb, Lower Thumb and Lake shore. Several were seen, some within a few feet. Others were heard. These showed no fear of man, and were often threatening in action though none actually charged. Care must be observed on all these streams. Suggest police whistle or small mouth siren . . . to announce presence. Shouting of no value! The loss of fish to bear must be extremely high on these streams. Besides the countless carcasses seen, it was estimated *that fully 50 % of the living fish* in the stream bore marks of varying severity—made by bears claws (rarely by teeth). Many of these wounds would be fatal within a few hours—probably before spawning, for the bear show every evidence of preferring the brighter fish to the older, darker ones.[82]

Bears were abundant at Karluk Lake in 1944, and Shuman's assistant noted "we estimated that bears kill and eat 240,000 fish out of this system."[83] Whenever Shuman surveyed the spawning areas in 1943–46, he found the waters and stream banks littered with bear-killed sockeye, especially in the small creeks. This apparent major source of sockeye mortality and the ever-declining runs alarmed Shuman, causing him to study bear predation at Moraine Creek in 1947, followed by a second study with Nelson at Moraine and Halfway creeks in 1948. When Shuman published the 1947 predation study (Shuman, 1950), his recommendation to control the bear population created such public controversy that the 1948 study was never formally published (Nelson et al., 1963).

Adult brown bear and four cubs, Karluk Lake tributary, 1949. (Richard F. Shuman, from John B. Owen, Grand Forks, ND)

In his last year at Karluk (1949), Shuman tried to build a permanent two-way weir on the Karluk River just below the lake's outlet. This weir was intended to count up-migrating sockeye adults and down-migrating smolts, but logistical and mechanical problems prevented its construction. Nevertheless, Shuman understood the importance of measuring both the sockeye escapement and smolt out-migration, goals that were finally achieved in the 1950s and 1960s by other biologists.

During Shuman's leadership of the Karluk studies in 1943–49, the ease and mode of travel greatly changed. Initially during the war years, biologists traveled to and from Alaska on commercial steamships or FWS vessels and these were under tight military control.[84] It was not until 1946 that biologists flew on commercial or naval airplanes between Seattle, Anchorage, and Kodiak, yet access to Karluk Lake remained nearly the same as for Bean's 1889 visit. In 1944 Shuman and his crew received no assistance from airplanes in moving supplies to the lake, though they occasionally saw military planes overhead. Because of the lake's remoteness, the FWS discussed in 1946 the need for a road to connect Larsen Bay and Karluk Lake, but air travel was then becoming more common around Kodiak Island and naval planes frequently landed at the lake to let their crews sport fish. In late 1946 a FWS official flew to Karluk Lake in a Waco amphibious airplane to visit the weir and research station. While the airplane was briefly available, gasoline

[82] See footnote 74.

[83] Jerre Olson 1944 notebook (18 July). Original notebook in personal papers of Jerre Olson, Auke Bay, AK.

[84] Jerre Olson, Auke Bay, AK, personal commun. with Richard L. Bottorff, 1997.

U.S. Fish and Wildlife Service Grumman Widgeon N 728 (left) and Grumman Goose NC709 (right), Karluk Lake, 1949. (E. P. Haddon, U. S. Fish and Wildlife Service, National Digital Library, FWS-933)

and supplies were flown to Karluk Lake; this one 45-minute round trip from Larsen Bay saved the biologists six laborious river trips. Finally in 1947, the Karluk research program was supported by frequent air transport of supplies and personnel directly to the lake by several FWS Grumman Goose and Widgeon amphibious airplanes. Thereafter, airplanes provided the main access and supply to Karluk Lake. Without a doubt, solving this huge logistical problem greatly expanded the scope of research possibilities for Karluk's biologists.

During Shuman's years at Karluk, communication between remote field locations and more-populated sites around Kodiak Island was done by short-distance radio, though direct radio contact between Karluk Lake and the FWS Kodiak headquarters was seldom possible. Instead, messages were relayed by people located at closer and more powerful radio stations (Larsen Bay and Karluk Village) or aboard boats around the island. During this period, Archie "Scotty" Brunton, an employee of the Larsen Bay cannery (radio KOT), often forwarded messages to Kodiak for the biologists at Karluk Lake since their 1.5 watt U.S. Forest Service radio had a range of only 25 km.[85]

Richard Shuman's career as a FWS fishery biologist ended tragically when he died in an airplane crash in southeast Alaska on 1 September 1954. Shuman received a fitting tribute to his memory and fisheries work in Alaska by the official naming of Mount Shuman, which towers over the southern half of Karluk Lake.

Several important federal actions impacting Karluk salmon fishermen and canneries were made during Shuman's years as research leader. In 1943 Secretary of the Interior Ickes established the Karluk Reservation for the Alutiiq people (Public Land Order 128). This reservation included 35,000 acres (14,164 hectares) of land and water near Karluk Village and the beach seining sites on Karluk Spit. The reservation boundary included the ocean waters 3,000 feet (914 m) from shore. For many years, the APA had dominated the fishing at Karluk and the Alutiiq fishermen had been excluded from prime beach seine locations, causing impoverishment for local residents (Grantham, 2011). Despite the reservation order, conflicts continued between beach seiners and purse seiners over access to the ocean waters within the boundary. Non-Alutiiq fishermen believed they could not be denied access to this fishing area because of provisions in the White Act. When federal fishing regulations in 1946 allowed only Alutiiqs to fish within the boundary, a lawsuit, *Hynes v. Grimes Packing Co et al,* was brought to settle the issue. In 1949 the U.S. Supreme Court (337 U.S. 86) ruled that 1) Secretary of Interior was authorized to establish the Karluk Reservation, and 2) Karluk inhabitants could not bar access to the waters and fish within the reservation.

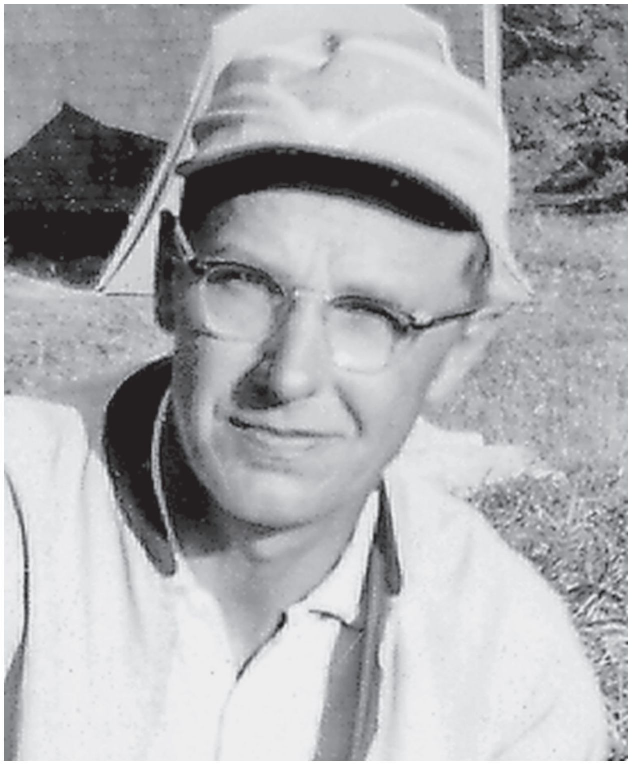
Philip R. Nelson

1946–56

Philip R. Nelson, FWS and BCF fishery biologist, studied Karluk's sockeye salmon for 11 years, first assisting Shuman in 1946–49 and then leading the research in 1950–56. Nelson, a graduate of the School of Fisheries, University of Washington, served in the military before working at Karluk. His research at Karluk comprised four main topics—stickleback life history, Bare Lake fertilization experiment, survival of gill-net-marked sockeye salmon, and sockeye salmon egg survival. In 1955, during Nelsons's later years at Karluk, the Fish and Wildlife Service split into the Bureau of Commercial Fisheries (BCF) and Bureau of Sport Fisheries and Wildlife.

During the four years he assisted Shuman, Nelson actively participated in all of the ongoing Karluk studies and was largely responsible for some. Routine tasks included installation and operation of the weir, collection of run composition data, surveys of sockeye spawning sites, and collection of limnological data. Nelson and Shuman jointly did the tagging studies on adult sockeye during 1946–48 to determine their travel time,

[85] Letter (24 October 1998) from Arthur Freeman, Indianapolis, IN, to Richard L. Bottorff, South Lake Tahoe, CA.



Philip R. Nelson (1918–). (Philip R. Nelson, Largo, FL)

one-month ripening period before spawning, and dispersion to specific spawning sites. Nelson also made major contributions to the bear predation studies at Moraine and Halfway creeks in 1947 and 1948, though Shuman apparently initiated both studies. They jointly prepared a manuscript on the 1948 bear predation study ("Further studies of bear depredations on red salmon spawning populations in the Karluk River system, 1948"), but it was not published.[86] Following Shuman's death in 1954, Nelson and several colleagues modified the 1948 bear predation manuscript several times and tried for over 10 years to publish it, without success (Nelson et al.. 1963). Despite this one lapse, Nelson, in contrast with many other biologists at Karluk, managed to publish most of his research.

An early research effort by Nelson was his life history investigations of threespine sticklebacks at Karluk Lake. He pursued this topic after Shuman and Rich refocused the Karluk research program in 1946 onto the factors that affected juvenile sockeye and the lake's limnology. Since the huge population of sticklebacks in the lake appeared to be serious competitors of young sockeye, it was prudent to gather basic biological information on this species. As a result, Nelson began the life history studies in 1948–49 and irregularly continued them until 1956, eventually expanding them to include Bare Lake's sticklebacks. His investigation did not measure the competition between sticklebacks and young salmon, but it did gather basic biological data on sticklebacks (Greenbank and Nelson, 1959).

Perhaps Nelson's most ambitious and important research project during his tenure at Karluk was the artificial fertilization experiment at Bare Lake, a small lake 25 km southwest of Karluk Lake. This field experiment originated from Rich's 1946 recommendation that the FWS study Karluk Lake's limnology to better understand the linkages between salmon-carcass nutrients, plankton, and young sockeye. By 1947–49 the FWS was actively considering the enrichment of Karluk

Brown bear, Karluk Lake tributary, ca. 1950–54. (Charles E. Walker, Sechelt, BC)

Bare Lake cabin, June 1954. (Clark S. Thompson, Shelton, WA)

[86] Shuman, Richard F., and Philip R. Nelson. 1950. Further studies of bear depredations on red salmon spawning populations in the Karluk River system, 1948. FWS. Unpubl. report. 33 p. Located at NARA, Anchorage, AK.

Sockeye salmon smolts, Bare Lake, 1955. (Clark S. Thompson, Shelton, WA)

Bare Lake outlet, weir, and salmon research gear, 1954. (Clark S. Thompson, Shelton, WA)

Lake to improve its fertility and sockeye salmon production, but the consequences of adding artificial fertilizers to a large Alaskan lake were then unknown.[87] Therefore, in 1949 they decided to first test the lake enrichment idea on a small lake before attempting it at Karluk Lake. To get the project underway, Nelson and Shuman searched Kodiak and Afognak islands for a suitable experimental lake and after a brief survey of possible sites selected Bare Lake in July 1949.

Nelson was fully responsible for the fertilization experiment at Bare Lake, though he collaborated with Professor W. T. Edmondson of the University of Washington and was assisted by many FWS officials and field employees. Each summer for seven years (1950–56), he added artificial fertilizers to Bare Lake and monitored the lake's chemical and biological response, especially that from its sockeye salmon (Nelson and Edmondson, 1955; Nelson, 1958, 1959). Fertilization rapidly increased the lake's photosynthetic rate and phytoplankton populations, which decreased water transparencies and increased pH values. Zooplankton populations did not immediately increase, but were much more abundant by 1957 (Raleigh, 1963). For the sockeye salmon, fertilization increased juvenile growth, smolt size, and ocean survival, but the number of returning adults seemed to be unaffected. Populations of juvenile coho salmon and resident Dolly Varden may have increased during the fertilization years, but stickleback growth rates did not increase (Nelson, 1959; Raleigh, 1963).

In many respects, Nelson's fertilization experiment at Bare Lake was a huge success, showing that lake enrichment increased juvenile sockeye growth, smolt size, and ocean survival. The ultimate desired result—greater numbers of returning adults—did not occur, perhaps because of factors beyond the influence of the nursery lake. In fact, since Bare Lake had a rather small original run of sockeye salmon, the number of returning adults was always highly vulnerable to chance events of commercial fishing, marine factors, and low flows in Bare Creek. In any event, this fertilization study was an innovative test of the linkage between lake nutrients and salmon production in an Alaska lake. The Bare Lake experiment was an important first step for the lake enrichment idea to become an accepted method for enhancing and rehabilitating depleted stocks of sockeye salmon in Alaska. Though the FWS initially planned the Bare Lake experiment as a prelude to fertilization of Karluk Lake, the idea was eventually discarded as new research topics at Karluk Lake became dominant. Nevertheless, in 1986–90 the ADFG fertilized Karluk Lake to enhance its fertility and sockeye salmon.

In another project, Nelson and his assistant Carl E. Abegglen measured the survival of gill-net-marked sockeye salmon at Karluk in 1953 (Nelson and Abegglen, 1955). This study responded to concerns that commercial gill nets may cause a greater loss of sockeye salmon than revealed in the catch statistics. That is, fish that escaped from a gill net with body injuries may later die unrecorded. To investigate this problem, Nelson and Abegglen trapped thousands of adult sockeye in Karluk Lagoon in 1953 and subjected them to varying

[87] Discussions within the FWS about the value of fertilizing Karluk Lake included Shuman and Nelson, and higher officials such as Elmer Higgins (Chief, FWS Division of Fishery Biology), Lionel A. Walford (FWS Director of Research), George B. Kelez, (Chief, FWS Alaska Fishery Investigations), Ralph P. Silliman (Chief, FWS Section of Anadromous Fisheries), and Clarence J. Rhode (FWS Regional Director).

degrees of physical damage from gill nets. Injured fish were tagged and released, along with a group of uninjured control fish, to proceed up the Karluk River. The study showed that 10–20% of the fish that escaped gill nets died from their injuries and mortality increased with wound severity. Yet, they found no difference between damaged and control fish in their travel times between the lagoon and the weir and between the weir and the spawning grounds.

Nelson and his assistants devoted considerable effort during 1947–53 to a study of the development, density, and survival of sockeye salmon eggs buried in various spawning substrates at Karluk. They regularly dug into spawning redds to assess the condition of the eggs. To monitor the seasonal development of eggs, they placed some inside baskets or cartridges and re-buried them in creek substrates; the containers were periodically retrieved and examined to assess the state of the eggs. At times the biologists found numerous leeches and oligochaete worms in the substrate and suspected that these invertebrates were destroying many eggs. Despite their labors and the reams of data collected, the outcome of the egg study was unclear, and, as a result, this research never was formally published or summarized in FWS reports.

William Francis Thompson (1888–1965). (From Stickney, 1989, University of Washington, School of Aquatic and Fishery Science, Seattle, WA)

William F. Thompson

1948–58

William Francis Thompson had a long and productive career as a fishery scientist and educator on the Pacific Coast of the United States and Canada in the early and mid 1900s (Stickney, 1989; Dunn, 2001a, b, c). He first investigated several of the most important marine fisheries in California and British Columbia, including halibut, herring, sardines, and albacore tuna, before focusing his scientific talents on Pacific salmon. Educated at Stanford University, he earned his B.A. (1911) and Ph.D. (1930) degrees while working with two eminent ichthyologists, David Starr Jordan and Charles H. Gilbert (Dunn, 2001a). For much of his fisheries career, Thompson was associated with the University of Washington (1930–58), first as Director of its School of Fisheries and later as Director of its Fisheries Research Institute (FRI).

Thompson's involvement with sockeye salmon research at Karluk began soon after he founded the FRI at the University of Washington in 1947. This institute, which had the goal of improving the scientific foundation of management of Alaska's salmon fisheries, was formed in response to concerns by the salmon packing industry about the depleted salmon runs, especially those at Bristol Bay. Initially, the salmon packing industry funded FRI's studies at Bristol Bay and other areas of Alaska, but as the scope of this research program expanded, by the mid 1950s this private source was inadequate and new funding sources were secured from the federal government, and later, from the State of Alaska (Stickney, 1989; Dunn, 2001a). The FRI began their studies of Karluk's sockeye salmon in 1948 and continued these until 1958 under Thompson's guidance.

Thompson was an important figure in the fisheries research history of Karluk for two reasons—his management of FRI research and his ideas about Karluk's sockeye salmon. First, Thompson actively directed the Karluk field research of FRI biologists Donald Bevan and Charles Walker, often recommending topics to investigate and offering advice as the sockeye studies progressed. Though he personally never did fieldwork at Karluk, Thompson annually visited each FRI research station for a few days and maintained an active interest

in the ongoing operations, progress, problems, and results of each project. He set high standards for the salmon research and expected scientifically sound results from his field biologists. The field notebooks of FRI biologists document that he was a major intellectual force in the planning and operation of FRI's salmon studies in Alaska.[88] Specifically, he secured funds for FRI's studies of the ocean migration routes (1948–49) and subpopulations (1950–54) of Karluk's sockeye salmon, both important and largely unexplored topics at the time. Thompson also acquired funds for a long-term study of juvenile sockeye salmon in Karluk Lake (1950–54) and for the first attempts to measure smolt out-migration from the lake. Thus, Thompson was a major influence on the planning and progress of FRI research at Karluk during 1948–58.

Second, Thompson was important in the research history for his insightful ideas on sockeye salmon biology and the commercial fishery. In particular for Karluk, he presented these ideas in an influential talk given at the National Research Council in Washington, DC, on 9 November 1950. In his presentation entitled "Some salmon research problems in Alaska," he stated his belief that Karluk's sockeye salmon had many independent subpopulations, a topic largely uninvestigated. Further, he claimed that the seasonal distribution of adult sockeye salmon that returned each year to Karluk had been greatly modified by past commercial fishing. To demonstrate this impact, he used early case pack records (1895–1919) from a single Karluk cannery to show that the run had shifted over the years from a unimodal to bimodal seasonal pattern. Thompson argued that adult sockeye returning during the midseason (15 July–31 August) were originally the most abundant and productive part of the Karluk run, but that the fishery had depleted these fish and left only the early and late runs. Furthermore, he reasoned that the loss of productive midseason fish may explain the overall long-term decline in sockeye salmon numbers at Karluk.

If Thompson's ideas were true, fishery managers needed to change their regulations to better protect midseason fish. Without a doubt, his idea about overharvested midseason subpopulations soon led to changes in the Karluk research programs of the FRI, FWS, and BCF. In particular, Bevan did a detailed study of the ages, sizes, and specific spawning habitats of midseason fish during 1950–54 and a few years later Owen attempted to measure the productivity of these subpopulations. Thompson's 1950 presentation, though never formally published, was issued as an FRI Circular (Thompson, 1950). In October 1951 Thompson again presented his analysis of Karluk's sockeye salmon at a meeting of the International Council for the Exploration of the Sea, Amsterdam, The Netherlands (Thompson, 1951).

In the years since Thompson presented his ideas on the subpopulations and run distribution of Karluk's sockeye salmon, the existence of subpopulations has been well substantiated. He certainly deserves great credit for focusing the attention of fishery biologists onto this biological feature of salmon and for stimulating considerable research on this topic in the 1950s and 1960s. Yet, questions remain about the original run distribution of Karluk's sockeye and whether past harvests of the commercial fishery produced the current bimodal seasonal pattern. Present fishery managers must deal with the reality of a bimodal sockeye run that has existed for at least 90 years and the fact that midseason fish never increased in abundance when protected from commercial fishing. Thus, Thompson's ideas on the original run distribution of Karluk's sockeye salmon have yet to be validated.

Thompson believed in the early 1950s that wooden picket weirs installed across a river to count salmon might harm these migrating fish by being a barrier to their free movements. Instead, he claimed that counting towers had significant advantages since they did not have a physical structure in the river that impeded the movements of sockeye adults and fry. Undoubtedly at Thompson's suggestion, Bevan and Walker explored the Karluk River in 1955 to find a suitable tower site and made several trial counts on the lower river. Soon thereafter, the FRI ended its sockeye research at Karluk, but Thompson's ideas about weirs eventually led to changes in the location, type, and operations of the counting structures used by the FWS, BCF, and ADFG. For example, the BCF replaced their traditional picket weir at Karluk with a counting tower in 1958–59, but after experiencing many problems that decreased the accuracy of the salmon counts, they returned to the picket weir in 1960. To further address concerns about the weir, they modified the structure in the 1960s to aid the upstream migration of sockeye fry. Van Cleve and Bevan (1973), both colleagues of Thompson at the Univer-

[88] Donald E. Bevan 1948–55 notebooks and Charles E. Walker 1950–55 notebooks. Located at FRI Archives, University of Washington, Seattle, WA.

sity of Washington, also believed that Karluk's weir harmed its sockeye salmon and recommended its removal from the upper river spawning area. In 1976 the ADFG moved the weir to the lower Karluk River, in part because of the concerns initially voiced by Thompson.

Thompson (1950) stated that sockeye salmon in the Karluk River and other river systems of the Pacific Coast were resilient to the effects of heavy commercial fishing and that these fish populations would respond to proper management:

> [Concerning the management of salmon fisheries] In fact, such resilience is the only explanation possible for the continuance of great runs into the Sacramento, the Columbia, the Fraser, the Karluk, and Bristol Bay despite tremendous fisheries over three-quarters of a century. This should give regulatory authorities in Alaska the courage to experiment. Every year is not a life and death crisis.

In 1954 he criticized the existing regulatory quota system used to harvest sockeye salmon at Karluk, where 50% of the total run must be allowed to escape to the spawning grounds. Further in 1955, he suggested that the FWS should experiment with the fishery regulations to get dramatically different harvests in alternate years (Thompson et al., 1954; Thompson and Bevan, 1955). He recommended greater commercial fishing on Karluk's spring-run sockeye and less on the midseason run. Apparently, these management ideas were not adopted, but Thompson showed a willingness to experiment with the fishing regulations to halt the long-term decline of its sockeye salmon. Ideally, he wanted regulations that permitted adequate escapements from all sockeye subpopulations. In this way, the full natural biological diversity of Karluk's sockeye salmon would be preserved to give them long-term resilience to fishery harvests and environmental challenges (Thompson, 1950).

In summary, Thompson was a remarkable individual in Karluk's fisheries history because his impact came from the force of his ideas and the guidance and inspiration he gave to other biologists. His intellectual energy extended well beyond his immediate sphere of influence at the FRI and included many other fishery biologists, agencies, commissions, and commercial interests. In contrast to most biologists in this history, he did not do field studies at Karluk, nor did he formally publish papers on its sockeye salmon. Nevertheless, he profoundly influenced the direction of sockeye salmon research at Karluk for many years.

Donald E. Bevan

1948–58

Donald E. Bevan maintained a deep interest in the salmon fisheries of Kodiak Island for his entire 50-year professional career as an FRI research biologist and Professor in the College of Fisheries, University of Washington. This region of Alaska and its fishes had fascinated him ever since he intensively studied the sockeye salmon at Karluk as a young biologist during 1948–58. After serving in the military (1942–46) in World War II as an artillery officer in Europe and being awarded the Purple Heart and Bronze Star, Bevan returned to civilian life and studied at the University of Washington, receiving his B.S. degree in fisheries in 1948. That same year, the FRI hired him as a research associate and project leader of the Kodiak Island research program, which then investigated the sockeye salmon at Karluk. He continued to study its sockeye salmon until 1958, after which he shifted his main research interests to the pink salmon

Donald Edward Bevan (1921–1996). (From Stickney 1989, University of Washington, School of Aquatic and Fishery Science, Seattle, WA)

of Kodiak Island. His sockeye salmon studies at Karluk were centered on four main subjects: ocean migrations of returning adults, sockeye subpopulations, Karluk Lake's limnology, and a review of historic salmon catches.

The ocean migration routes and home-stream composition of adult sockeye salmon that traveled from the Gulf of Alaska through Kupreanof Strait and along the west coasts of Afognak and Kodiak islands were poorly known in the mid-1940s. In particular, were these west coast sockeye salmon homing just to the Karluk River, to several other local home streams, or to more distant streams on Alaska's mainland? If these salmon were composed of multiple stocks, what proportion went to each home stream and how did the proportions change throughout the run season? Knowledge of these ocean migrations was crucial to the proper management of these salmon, since commercial fishing along the west coast potentially intercepted fish homing to the Karluk River. Indeed, an earlier tagging study at Uganik Bay in 1927 suggested that Karluk River fish were being caught well before they reached the Karluk District (Rich and Morton, 1930).

Bevan's first research project at Karluk (1948–49) investigated the ocean migrations and homing of adult sockeye salmon on the west coast of Kodiak and Afognak islands. In the first year, he tagged nearly 4,000 adult sockeye along the northwest coast of Kodiak Island in June–August 1948 and then searched the area for recoveries (Bevan. 1959, 1962). The vast majority of sockeye tagged between Afognak Island and Cape Karluk, in fact, homed to the Karluk River, with very few recoveries found in distant areas. In the second year, he tagged more than 7,000 fish from four sites on the northwest coast of Kodiak Island in June 1949. Because his results from the previous year showed there was little mixing of sockeye stocks, he used the 1949 tagging and recovery data to estimate Karluk's total sockeye run. He found that the tagging process altered the sockeye's migratory behavior for about 48 hours. Spring-run fish typically reached the Karluk River weir, then located at the lake's outlet 40 km upstream from the ocean, about nine days after they were tagged in the ocean. Bevan (1959) used his 1948–49 tagging studies for his Ph.D. dissertation at the University of Washington.

In 1950 Bevan began a detailed study of sockeye salmon subpopulations at Karluk, gathering run composition data (age, length, and sex) to see how these factors varied seasonally in the commercial fishery and at different spawning sites.[89] Some initial data had already been collected in 1948–49, but he greatly intensified his efforts in 1950–54 and sampled many thousands of adult sockeye at the canneries, river weir, and lake spawning grounds. Even after the FRI curtailed their active studies at Karluk Lake in 1954, Bevan continued to collect this run composition data at Karluk's canneries until 1958. Although it is difficult to find in the Karluk and FRI literature a clear statement of Bevan's goals for these adult sockeye studies, he apparently wanted to document the existence of subpopulations and learn which groups were most heavily harvested in the commercial fishery. Of course Thompson, Bevan's immediate supervisor and mentor, strongly believed that sockeye salmon subpopulations existed. To pursue this idea, Bevan prepared hundreds of length-frequency graphs of sockeye sampled from diverse locations and seasons at Karluk, and, indeed, these showed distinct size differences between spring- and fall-run fish.[90] On an even finer level, sockeye that homed to specific spawning habitats at Karluk Lake also had definite size differences. While previous Karluk biologists (Barnaby, DeLacy, Shuman, and Nelson) knew about these size variations and the seasonal segregation of the sockeye runs, Bevan collected massive amounts of scientific data on these dissimilarities. Unfortunately, he failed to publish his subpopulation evidence, causing later biologists to repeat this work for at least the next decade. At the time, scientific proof of subpopulations in Karluk's sockeye salmon would have been a major accomplishment.

Besides collecting run composition data, Bevan and Walker regularly surveyed the spawning habitats of sockeye salmon at Karluk Lake during 1948–54 (Bevan, 1953; Bevan and Walker, 1954, 1955).[91] During their first inspections in 1948–49, they described the physical features of each spawning tributary and explored upstream to the limits of salmon migration, usually an impassable waterfall or cascading barrier. Typically, they surveyed these habitats every week,

[89] Donald Bevan and Charles Walker assisted each other in the field at Karluk and collaborated on their respective adult and juvenile sockeye studies.

[90] All of Bevan's run composition data on Karluk River sockeye salmon for the period 1948–58 are stored in the FRI Archives, University of Washington, Seattle. These include original data sheets of length and sex, scale impressions, and tapes used in the fish-measuring machines.

[91] Bevan, Donald E. 1951. Karluk Lake stream surveys, 1948–1951. Kodiak Island Research Group, FRI, University of Washington, Seattle, WA. Unpubl. report. 45 p. Located at FRI Archives, University of Washington, Seattle, WA.

Donald Bevan, Karluk Lake, ca. 1952. (Charles E. Walker, Sechelt, BC)

but in some years and locations they made regular inspections every few days. Consequently, they amassed accurate records of when sockeye used the different spawning habitats over the full spawning season. Their surveys revealed a distinct, repeatable pattern of use each year—early-run sockeye spawned in lateral and terminal tributaries, while middle- and late-run sockeye spawned in terminal streams, lake beaches, and the upper Karluk River. This repeatable segregation of sockeye runs by spawning habitat and season implied the existence of subpopulations, but Bevan and Walker presented their survey data in FRI reports without comment.

Bevan and Walker also collected limnological data at Karluk Lake during 1948–54. In the first four years, they simply measured surface water temperatures wherever they traveled, but in the next three years they collected weekly depth profiles of water temperature and transparency in all three of the lake's internal basins (Bevan, 1953; Bevan and Walker, 1954, 1955). They monitored the lake's water level and river's flow in 1952–54 and plotted a discharge-rating curve for the Karluk River (Bevan and Walker, 1955). Also during this period, they recorded climatological data at the lake research station. In 1952 Bevan briefly studied the lake's phytoplankton and zooplankton for a limnology class he took at the University of Washington.[92]

To aid his study of Karluk's sockeye salmon, Bevan collected and microfilmed historic case-pack records from many salmon canneries on Kodiak Island, a job he was uniquely positioned to do since the salmon canning industry funded his research.[93] In 1953 he examined these data to learn if sockeye salmon in the early fishery had been transported to the Karluk canneries from other areas of Kodiak Island and the Alaska Peninsula.[94] If these imports were large, the number of fish attributed to Karluk's run might be erroneously high. Indeed, he found that sockeye caught at Red River, Little River, and Uganik Bay had been transported to Karluk's canneries and added to its catch statistics, especially in June–July, but transfers from Chignik and Alitak were minor. After removing non-Karluk fish from the Karluk catch statistics, the seasonal catch distributions in these early years became more bimodal, though many midseason fish were still present.

The FRI ended its sockeye salmon studies at Karluk Lake after the 1954 field season, but Bevan and Walker spent part of 1955 searching for a suitable counting tower site on the Karluk River. They wanted to briefly operate a counting tower to learn if it was superior to the traditional wooden picket weir. At the time, Thompson and Bevan, and perhaps Walker and Van Cleve, believed that the picket weir at the lake's outlet harmed sockeye adults and fry. Bevan and Walker temporarily operated a counting tower at Karluk Lagoon and the Portage in 1955, but various problems caused them to abandon the idea.

Despite Bevan's many years of research on Karluk's sockeye salmon, he formally published only two papers on the topic: the 1948–1949 tagging study and an analysis and discussion of the historic decline of its sockeye runs (Bevan, 1962; Van Cleve and Bevan, 1973). In the 1973 paper, Bevan provided detailed field knowledge about Karluk's sockeye, while Van Cleve

[92] Bevan, Donald E. 1952. Karluk Lake plankton. Kodiak Island Research, FRI, University of Washington, Seattle, WA. Unpubl. report. Located at FRI Archives, University of Washington, Seattle, WA.

[93] Microfilm rolls containing historic catch records for Karluk area canneries are located in the FRI Archives, Seattle, WA. This microfilm collection contains many records, reports, and statistics, including cannery catches, case packs, APA superintendent's reports, APA hatchery operation reports, USBF and FWS reports, stream surveys, escapement counts, and ocean tagging data.

[94] Bevan, Donald E. 1953. The effect of red salmon catches from nearby streams on the Karluk pack. *In* Rae Duncan, Karluk, Packs of red salmon, 1895–1930. FRI, University of Washington, Seattle, WA (April 21, 1953). Unpubl. report. 26 p. Located at FRI Archives, University of Washington, Seattle, WA.

Donald Bevan (left), Kim Clark (center), and Charles Walker (right), Karluk Lake, ca. 1952. (Charles E. Walker, Sechelt, BC)

had only briefly visited the research station.[95] Besides the two formal papers, Bevan produced over 40 unpublished reports during 1950–85 that contain data on Karluk's salmon. Most of these reports were issued as FRI Circulars that summarized his annual surveys of pink salmon on Kodiak Island.[96] Yet some of the FRI Circulars from the 1950s contain data on Karluk Lake's limnology, stream surveys of spawning sockeye salmon, and daily weather conditions. His 1953 unpublished report on the historic harvests of sockeye salmon from areas near Karluk was insightful for understanding the original run distribution.[97] Sometime after 1955 Bevan and Walker prepared a summary report of all FRI studies on Karluk's sockeye salmon, but the location of this document remains unknown.[98]

It is unclear why Bevan did not produce additional formal publications on Karluk's sockeye salmon, most notable being his subpopulation results of 1950–54. Possibly, he may have been influenced by Thompson, who held high research standards and wanted a complete examination and understanding of a fisheries question before publication. Bevan's heavy work load, which then included his studies of Kodiak Island's pink salmon in 1958 and completion of his Ph.D. dissertation in 1959, may have prevented publication of these earlier studies. Nevertheless, Bevan's research accomplishments on Karluk's sockeye salmon were substantial.

Charles E. Walker

1950–55

Charles Edward Walker spent six field seasons (1950–55) at Karluk as a FRI fishery biologist, his primary interest being the freshwater life stages of juvenile sockeye salmon.[99] He wanted to understand all stages of the early life history of these fishes from the time when alevins or fry emerged from their gravel incubation sites, until several years later when they left the lake as smolts for the ocean. Specifically, Walker wanted to document the time of fry emergence from spawning gravels and their migration to Karluk Lake, the distribution and movements of juveniles in the lake, the sizes and summer growth rates of these lake residents, the effects of environmental factors on juveniles, and the smolt sizes, ages, and times of migration to the ocean. Thompson was eager for these studies because he believed that previous biologists had incorrectly aged the young fish at Karluk, counting false annuli and, thus, recording scale ages that were too old. In fact, the sockeye salmon

[95] Bevan's field research on Karluk River sockeye salmon was greatly aided during 1948–58 by many competent field assistants, including John Bridgeman, Rae Duncan, Allan C. Hartt, Edward S. Iversen, John W. Martin, Wesley J. Morgan, William Mulligan, Wallace H. Noerenberg, Clinton E. Stockley, Fredrik V. Thorsteinson, Charles E. Walker, and Raymond A. Willis.

[96] FRI Circulars were distributed to several fisheries libraries in Alaska and along the Pacific Coast, making them somewhat more accessible to biologists than most unpublished reports.

[97] See footnote 94.

[98] According to Charles Walker, only three copies of this summary report were prepared—one for Bevan, one for Walker, and one for FWS biologist Robert F. Raleigh. Walker and Raleigh's copies have since been lost and the location of Bevan's copy is unknown. A copy of the summary report may exist in Donald E. Bevan's papers, Manuscripts and University Archives Division, University of Washington Libraries, or the FRI Archives. We mention this unpublished report because of its potential importance to the Karluk research history. Letter (10 October 1996) from Charles E. Walker, Sechelt, BC, Canada, to Richard L. Bottorff, South Lake Tahoe, CA.

[99] Walker, Charles E. 1954. Karluk young fish study, 1950–1954. Kodiak Island Research, FRI, University of Washington, Seattle, WA. Unpubl. report. Located at FRI Archives, University of Washington, Seattle, WA.

Charles Edward Walker (1921–   ). (Charles E. Walker, Sechelt, BC)

smolts at Karluk were then considered to be unusual because they migrated seaward in their third and fourth years, much older than had been recorded for most other sockeye systems.

Walker diligently collected juvenile sockeye salmon from many locations at Karluk for five field seasons (May–October). He collected these fish with a wide range of sampling gear—various lengths and designs of beach seines, dip nets, hand seines, fyke nets, box traps, and trawls. Wherever he went at Karluk Lake, he looked for young sockeye and made notes on their presence, size, schooling behavior, and movements. He tried to collect juveniles from the limnetic zone of Karluk Lake by using a trawl, but the equipment operated poorly and no further attempts were made to sample the open-water habitat. Hence, most of his collections were made in the littoral zone of the lake or the shallow waters of tributary streams and the upper Karluk River.

Over the years, he made hundreds of beach seine collections and measured the size of thousands of young sockeye. Juvenile size, plotted as length-frequency diagrams, documented the first summer's growth of newly hatched sockeye fry as their lengths progressively increased from 25–30 mm in May to 50–60 mm in October. Unexpectedly, Walker observed a north–south gradient in juvenile size in Karluk Lake, with larger-sized fish at the north end. Since he rarely caught older and larger juvenile sockeye in the lake's littoral, and failed to sample the limnetic zone, he realized his studies were incomplete. Even with these sampling limitations, his results on the early life stages were significant.

During several of his years at Karluk, Walker made a special effort to observe the spring emergence and migration of sockeye fry between their natal tributary streams and the lake. This part of the sockeye's early life cycle, however, was often difficult for biologists to examine because winter-like conditions often still prevailed into spring and the ice-covered lake prevented boat travel to the tributary streams. When Walker arrived at Karluk Lake on 5 May 1951, the lake was still ice-covered and the fry migration was already underway. In 1953 he successfully measured the fry emergence and migration in two Karluk tributaries; Halfway Creek had one migration period (May), while Canyon Creek had two periods (May and July). The migration patterns of these two streams differed because only spring-run sockeye spawners had used Halfway Creek the previous year, while both spring- and fall-run spawners had used Canyon Creek. That is, both egg deposition and fry migration had similar distributions, but these two events were separated in time by the egg-development period. About 10 months of development separated egg deposition and fry emergence in these tributary creeks. Walker also discovered that newly emerged sockeye fry in tributary creeks migrated downstream to the lake at night.

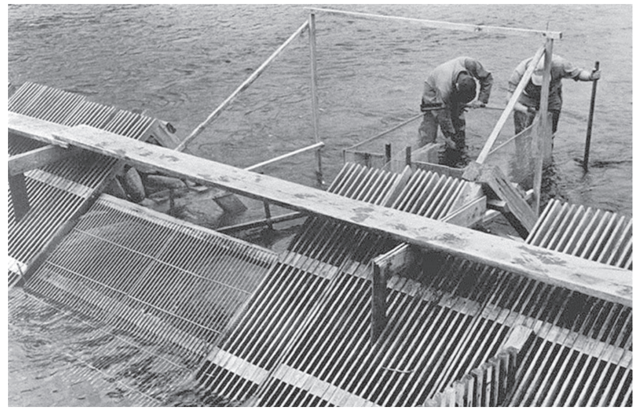
In direct contrast to the down-migrating fry of tributary creeks, sockeye fry in the upper Karluk River moved upstream toward the lake along both river banks. Further, these young sockeye migrated upstream

Beach seining for sockeye salmon juveniles, Karluk Lake, ca. 1952. (Charles E. Walker, Sechelt, BC)

U.S. Fish and Wildlife Service biologist Carl Abegglen (left) and Fisheries Research Institute biologist Charles Walker (right), Karluk River weir near Karluk Lake's outlet, ca. 1954. (William F. Thompson, Fisheries Research Institute, Seattle, WA)

in two periods, the first as newly emergent fry (28 mm length) in May and early June and the second as larger fry (47 mm length) in late July through August. The later migration showed that some young sockeye resided in the upper river for several months after emergence before moving to the lake. Fry inhabited the upper Karluk River as far downstream as the Portage, a slower reach of the river having dense growths of aquatic plants. Walker and Bevan expressed concern that the counting weir might impede up-migrating fry from reaching the lake, or perhaps bruise or damage these fish as they passed through the wooden pickets. Eggs spawned in the upper river needed about 8–8.5 months of development until the fry emerged, considerably less time than required in the tributary creeks and lake beaches.

One of Walker's goals of 1950–54 was to measure the composition and total production of sockeye smolts from Karluk Lake. Each spring, he observed these



Sockeye salmon smolt trap, Karluk River weir, 1954. (William F. Thompson, Fisheries Research Institute, Seattle, WA)

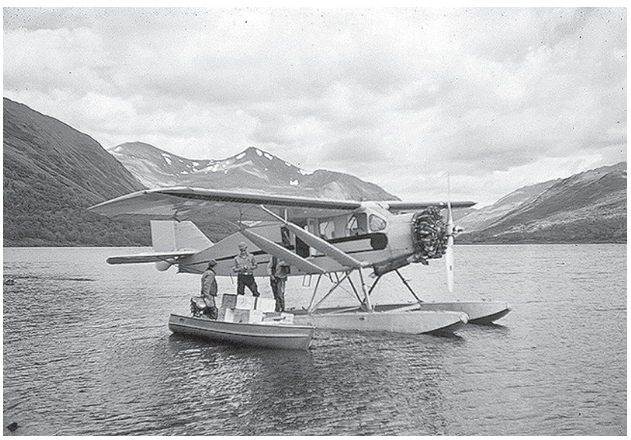
smolts at the lake outlet weir and recorded their downriver migration from late May to mid July. Two size and age groups of smolts predominated (3- and 4-year), with the larger smolts migrating earlier in the season. The overall migration peaked in the first three weeks. Both the FRI and FWS wanted to accurately measure the total smolt out-migration, but this was a daunting task given that adequate collecting gear and statistical protocols had yet to be developed.

In any event, Walker experimented in 1953 with several methods to measure smolt abundance. He first tried to concentrate the smolts into a small area as they left the lake and entered the upper river, and then to count them using a photographic method, but this system worked poorly. Eventually, he built smolt traps into the wooden picket weir to census the migration. The smolts were attracted to the trap opening because some of the wooden pickets were replaced with metal grates; this alteration increased the water flow through that weir section. Walker operated three smolt traps at the Karluk weir in 1954; trap catches gave him a smolt abundance index, but not an exact estimate of the total numbers. Nevertheless, the 1954 smolt traps were an important first step in the eventual development of an accurate method for measuring the total smolt out-migration.

In 1951 as Walker and Bevan watched the commercial beach seines being hauled ashore on Karluk Spit, they were surprised to see many sockeye salmon smolts also being incidentally captured in the nets.[100] They observed that the smolts easily escaped through the

[100] Walker, Charles E., and Donald E. Bevan. ca. 1968. Factors possibly contributing to the condition of the Karluk sockeye salmon run. Unpubl. handwritten report. 18 p. Located at FRI Archives, University of Washington, Seattle, WA.

Weather station, Karluk Lake, ca. 1952. (William F. Thompson, Fisheries Research Institute, Seattle, WA)



Unloading supplies for the research biologists, Karluk Lake, ca. 1952. (Charles E. Walker, Sechelt, BC)

net openings when few adult salmon were caught, but the young fish were unable to escape when many adults were present, the adult bodies blocking their exit. As the seine was hauled onto the beach, the frantically thrashing adult salmon destroyed most of the smolts.

During Walker's years at Karluk, he examined the stomach contents of predatory fishes and birds for juvenile sockeye, though it is unclear how many of these he sampled. He believed that newly emerged sockeye fry suffered substantial fish predation, but that larger juveniles did not; both coho salmon juveniles and charr (he called all charr at Karluk "Dolly Varden") preyed on the young sockeye. He claimed that small charr (90–180 mm) heavily preyed on juvenile sockeye, as did some larger charr in the upper Karluk River. Unexpectedly, he found a few large juvenile sockeye that had preyed on small sockeye. Of the bird stomachs he examined, mergansers rarely preyed on juvenile sockeye, but more commonly ate sticklebacks. While recording these food habits, Walker also examined the internal parasites of juvenile sockeye in 1953 and found roundworms in the pyloric caeca of 2-year fish and tapeworm cysts in the smolts.

In many respects, Walker's studies of Karluk's juvenile sockeye salmon were pioneering. With the exception of the previous smolt-marking studies of 1926–36, little had been previously published about these young salmon. Earlier Karluk biologists certainly realized the importance of understanding the freshwater life stages of sockeye salmon and had collected samples or made field observations, but many life history details remained unknown or unpublished. Walker also failed to publish his studies, but did present his results in several FRI reports[101] that were eventually used and cited by Van Cleve and Bevan (1973). His 1954 report was useful and circulated widely among Karluk's biologists.

Besides his sockeye salmon research, Walker devoted some time to life history studies of threespine sticklebacks at Karluk Lake.[102] Sticklebacks were very abundant lake residents in the 1950s, and Walker consistently caught many more of them in each beach seine than juvenile sockeye. He witnessed the stickleback mass migration in Thumb and O'Malley rivers in May–June and realized that these fish spawned in the shallow tributary lakes (Greenbank and Nelson, 1959). He also collected some large sticklebacks in Karluk Lagoon.[103] Walker was the first biologist since Rutter in 1903 to observe ninespine sticklebacks at Karluk Lake (Evermann and Goldsborough, 1907; Greenbank and Nelson, 1959).

Walker participated in all of the FRI research projects at Karluk Lake, and, in particular, helped Bevan survey the different spawning sites and age the adult

[101] 1) See footnote 99.
2) Walker, Charles E. 1956b. Karluk young fish study—scale graphs, 1950–1954. FRI, University of Washington, Seattle, WA. Unpubl. report.
3) Walker, Charles E. 1959. The enumeration of the Karluk red salmon smolt run in 1954. FRI, University of Washington, Seattle, WA. Unpubl. report. 15 p. All three reports located at FRI Archives, University of Washington, Seattle, WA.

[102] Walker, Charles E. 1954. Comments on the life history of Karluk Lake stickleback (Gasterosteus aculeatus). Kodiak Island Research, FRI, University of Washington, Seattle, WA. Unpubl. report. A reference to this report was located in the FRI Archives card catalogue, University of Washington, Seattle, WA, but we were unable to find a copy.

[103] Memo (20 August 1956) from Philip R. Nelson, Fishery Research Biologist, FWS, Seattle, WA, to John Greenbank, FWS, Juneau, AK. Located at NARA, Anchorage, AK.

sockeye salmon scales.[104] He routinely collected weather data and limnological samples at the lake. Camp Island served as the base of FRI operations in 1950–53, followed by facilities at the Karluk River weir in 1954. Transportation around the lake was by a small Aluma Craft skiff (4.3 m) and 10 horsepower Johnson outboard motor. Supplies were periodically flown to Camp Island via amphibious aircraft. In 1955 Walker and Bevan explored the entire Karluk River for a counting tower site and briefly tested several locations. While exploring the river, Walker added to his observations of sockeye juveniles and sticklebacks, and he collected both species in Karluk Lagoon.

In summary, Walker's studies of the juvenile sockeye salmon at Karluk Lake gave new information on their freshwater life; his work was the first detailed investigation of these young fish. Many previous biologists initiated brief studies of the early life stages, but little such data exists in Karluk's historical literature—surprisingly, more than 50 years after Walker's studies, much remains unknown about the juvenile sockeye salmon of Karluk Lake. Personally, Walker highly valued his years of field research at Karluk, claiming that it "provided me with the greatest learning experience of my life (in biology that is) and the lessons carried me throughout my career".[105]

Richard Van Cleve

Richard Van Cleve (1906–1984). (From Stickney 1989, University of Washington, School of Aquatic and Fishery Science, Seattle, WA)

Richard Van Cleve had a long and distinguished career as a fisheries research biologist and educator at the University of Washington, being appointed Director of the School of Fisheries in 1949 and then Dean of the College of Fisheries in 1958–71. During his many years at the University of Washington, Van Cleve undoubtedly followed the progress of ongoing FRI fisheries studies on Karluk's sockeye salmon and discussed the results with colleagues Thompson, Bevan, and Walker, but there is no evidence that he personally did field research there. Beyond his duties as a Professor of Fisheries, he occasionally served as a consultant to the FWS and BCF on their fisheries research in Alaska, and at times this included their studies of sockeye salmon at Karluk.

Van Cleve's main contribution to the knowledge about Karluk's sockeye salmon was his 1973 scientific publication with Bevan. At the time, Van Cleve was Professor Emeritus at the University of Washington. Their paper discussed the reasons for the historic decline of sockeye salmon runs at Karluk and offered ideas for rehabilitation. It summarized and analyzed both published and unpublished data, much of it from Bevan and Walker's field work of 1948–58, but also data from FWS and BCF biologists. Van Cleve and Bevan emphasized that many subpopulations were present, with perhaps the largest group being the fall-run stock that spawns in the upper river. They believed that the importance of the river-spawning subpopulation to the overall productivity of the Karluk run had not been fully appreciated and suggested protective measures

[104] 1) Walker, Charles E. 1955. Scale analysis, 1948–1953. University of Washington, FRI, Kodiak Island Research. Unpubl. report. Located at FRI Archives, University of Washington, Seattle, WA.
2) Walker, Charles E. 1956. Age analysis of the Karluk red salmon runs, 1922, 1924–1936, and 1952–1955. FRI, University of Washington, Seattle, WA (January 31, 1956). Unpubl. report. 29 p. Located at FRI Archives, University of Washington, Seattle, WA.

[105] Letter (5 April 1998) from Charles E. Walker, Sechelt, BC, Canada, to Richard L. Bottorff, South Lake Tahoe, CA.

for these fish. Further, they recommended that research on Karluk's sockeye salmon be curtailed and claimed that these activities harmed the productive midsummer runs that had already been depleted by heavy commercial fishing. Their recommendation to enhance midseason runs apparently had little impact on the ADFG fishery managers, who faced the reality of distinct spring and fall sockeye salmon runs.

When Van Cleve and Bevan's paper was published in 1973, the Karluk River weir was located just below the lake's outlet, and fall-run sockeye spawned in the river above and below the weir. Van Cleve and Bevan believed that the weir harmed the sockeye salmon by 1) restricting the natural to-and-fro homing behavior of fall-run river spawners, 2) slowing the downstream migration of smolts, and 3) impeding the upstream migration of newly emerged fry to the lake. Because of these potentially serious impediments, they recommended complete removal of the weir in order to aid rehabilitation of the sockeye salmon run. Thompson (1950) had previously argued that weirs interfered with salmon homing behavior, and Bevan and Walker searched the Karluk River in 1955 for a counting tower site to replace the traditional picket weir. During a brief visit to the Karluk research station in July 1957, Van Cleve expressed his concerns about the picket weir to the BCF field biologists and recommended the weir's removal.[106] His visit and recommendation convinced the BCF to substitute a counting tower for the wooden picket weir in 1958–59, though they soon returned to a picket weir. Many years later, Van Cleve and Bevan's 1973 paper helped convince the ADFG to move the 1976 weir to the lower Karluk River and away from the spawning habitat of fall-run sockeye salmon. This action returned the upper river to its natural, unfettered spawning condition.

It is unclear what stimulated Van Cleve's interest in Karluk's sockeye salmon since he never studied them in the field and only visited the FRI research station a few times. Perhaps it was his regular contact with Thompson, Bevan, and Walker and his desire to solve the long-standing fisheries question of what had caused the sockeye salmon decline at Karluk. He must have followed the progress of sockeye research by the FRI and FWS field biologists in the late 1940s and early 1950s. The 1973 paper was the culmination of views held for at least 20 years; many of the ideas likely originated from Thompson and were supported by Bevan and Walker's field studies.

George A. Rounsefell

1951–58

George Armytage Rounsefell worked as a USBF and FWS fishery scientist for 39 years (1925–63), followed by another 13 years as Professor of Marine Science at the University of Alabama (Rounsefell, 1977; Skud and Everhart, 1977). His interests in fisheries and marine science ranged over many topics and fish species, including Pacific salmon. Of his 89 career publications, nine dealt with Pacific salmon and three discussed or presented data on Karluk's sockeye salmon. Though Rounsefell never did field research at Karluk, he summarized and analyzed data collected by other USBF, FWS, and BCF fishery biologists.

Well before his direct involvement with the sockeye salmon research data from Karluk, Rounsefell followed the progress of the long-term field studies there through his professional contacts with fellow fishery biologists and former classmates of Stanford University. He was familiar with Alaska and its fisheries, hav-

George Armytage Rounsefell (1905–1976). (Brigham Collection BRI #845, Historical Photo Collection, Northeast Fisheries Science Center, National Marine Fisheries Service, Woods Hole, MA)

[106] John B. Owen 1957 notebook. Original notebook from the personal papers of John B. Owen, Grand Forks, ND; notebook to be donated to NARA, Anchorage, AK.

ing studied its herring during his early career with the USBF. As Acting Director of the USBF Fisheries Biological Station in Seattle in 1934, he regularly reported to higher officials on the progress of the sockeye studies at Karluk. These studies eventually came under his direct supervision in 1947–48 when he became the FWS Chief of the Branch of Anadromous Fisheries, and in that capacity he briefly visited the Karluk Lake research station in August 1947 to discuss the field work with Shuman.[107] Consequently, for many years, Rounsefell knew about the declining sockeye salmon runs and the attempts to find the cause. He was aware of the long-term research program at Karluk and the plans for future studies.

Of Rounsefell's three scientific publications on Karluk's sockeye salmon, his 1958 paper, which analyzed and discussed the causes of the declining runs, was a significant accomplishment that focused the attention of many fishery biologists on this productive salmon system. This paper indelibly linked his name to Karluk's sockeye salmon and altered the direction of field research there for many years. Yet it is unclear exactly when or why Rounsefell began his independent analysis of Karluk's sockeye salmon, though this occurred sometime in 1949–52 after Lionel Walford, FWS Director of Research, gave him the assignment. Obviously, Walford wanted FWS biologists to publish more papers from the large mass of data they had already collected. In any event, by December 1952 Rounsefell produced a preliminary manuscript, "Population dynamics of the sockeye salmon, *Oncorhynchus nerka,* of Karluk River, Alaska," with Shuman listed as junior author.[108] The 1952 manuscript had many topics of interest to fishery biologists; its major subject headings were:

The Problem
Normal seasonal occurrence of the runs
Age composition of the runs
Relations of migrant age and total age with the time of the runs
Estimation of numbers and age composition of the runs
Relation between season of smolt migration and ocean age
Spawning potential
  Fecundity
  Sex ratio
Seasonal trends in size at maturity
Relation of ocean temperature to size at maturity
Season of ocean growth
Relation of ocean growth seasons to size at maturity
Relation of ocean growth seasons to sex ratio
Fecundity of various age groups
Seasonal distribution of the escapement
Factors affecting the size of smolts
Relation between escapement, size of smolts, and returns
Interpretation of relations between escapements and returns
Conclusions
Recommendations
References

Shuman critically reviewed the manuscript, declined joint authorship, and recommended that it not be published. Ralph Silliman, FWS Chief of the Section of Anadromous Fisheries, also reviewed the manuscript and questioned the data analysis:

> My general comment is that the data have been almost over-analyzed. The extreme complexity of the analysis, the omission of the data which do not conform, and the use of highly derived estimates detract from the confidence which might be placed in the results for application to fishery regulation.[109]

Rounsefell continued to analyze the sockeye salmon data and revised the 1952 manuscript over the next 4–5 years until it was finally published in 1958.[110] By then the scientific paper, which still focused on the causes for the long-term decline of the sockeye salmon runs, had grown to over 80 pages, with many tables, graphs, statistics, and appendices. To restore Karluk's sockeye salmon runs, Rounsefell recommended eliminating predatory fishes, enhancing the midseason run, restoring natural

[107] See footnote 74.
[108] See footnote 80.

[109] Memo (6 March 1953) from Ralph P. Silliman, Chief, Section of Anadromous Fisheries, to Chief, Pacific Salmon Investigations. Located at ABL, Auke Bay, AK.
[110] A historical sidelight exists about Rounsefell's publications on Karluk's sockeye salmon. He prepared his 1952 Karluk manuscript while stationed at the FWS Woods Hole Laboratory, MA. Upon completing the manuscript and sending Shuman a review copy, Rounsefell departed for two years to Turkey as Leader of the Fishery Mission, Food and Agriculture Organization, United Nations. In early 1953, Ralph Silliman, FWS Chief of the Section of Anadromous Fisheries, sent a letter to FWS Chief of North Atlantic Fishery Investigations requesting return of the Karluk research data possessed by Rounsefell. The ultimate disposition of these important Karluk data is unknown. The Karluk research data to be returned included: 1) pink salmon escapements, 2) smolt migration data (1937–49), 3) Karluk Lake water levels (1931–50), 4) Karluk Lake thermocline charts (1921–47), 5) Kodiak weather records (1881–1951), 6) sockeye salmon escapements, catch, and total run (1937–50), 7) sockeye salmon age compositions and return from escapements, and 8) Karluk Lake weather records (1921–48).

cycles of abundance, fertilizing Karluk Lake, improving spawning habitats, and increasing egg deposition.[111]

Although the large size, format, and statistical analyses made Rounsefell's 1958 paper difficult for many fishery biologists to digest, it nevertheless had a great impact upon those involved in sockeye salmon research at Karluk. The paper received close scrutiny and generated heated discussions within the FWS and BCF, and was even the subject of departmental seminars and conferences as biologists and managers evaluated the paper's conclusions and debated how the research program should be altered. These discussions began within the FWS even before the paper's formal publication, as preliminary review copies circulated within the agency. Donald McKernan, FWS Administrator of Alaska Commercial Fisheries, stated in 1956 that Rounsefell's "findings are quite radical," but McKernan altered the management policies at Karluk to follow some of these new recommendations.[112]

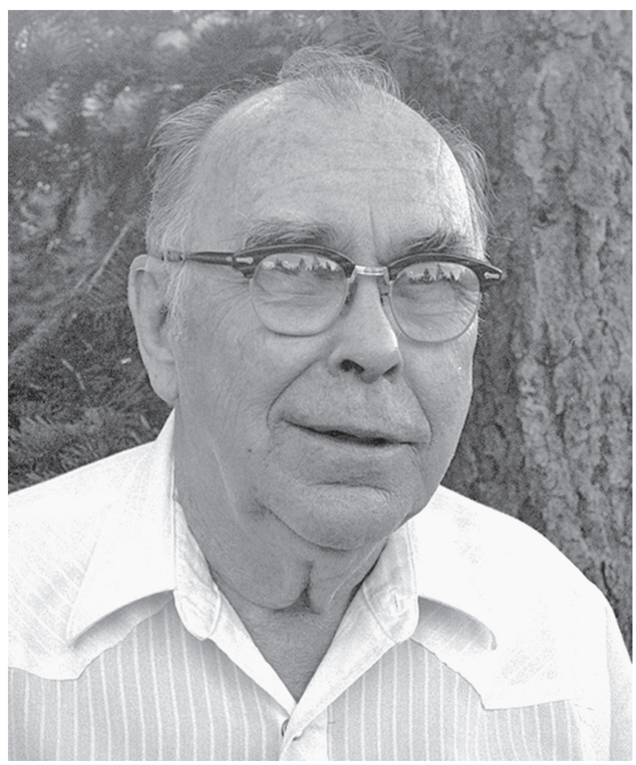
In challenging the then prevailing ideas about Karluk's sockeye salmon and in stimulating future research, Rounsefell's 1958 paper was a success. His paper intensified discussions about these salmon and motivated fishery biologists to either pursue some of the new ideas or design studies to disprove some of Rounsefell's conclusions. In particular, some biologists strongly disagreed with his claim that Karluk's sockeye salmon run was one population. Instead, they knew, after years of field observations and tagging studies, that at least the spring and fall runs were distinct subpopulations. And they suspected that even finer distinctions might exist for fish that appeared to home to specific spawning sites. To conclusively prove their point and highlight Rounsefell's error, several biologists actively pursued subpopulation studies in the years after the 1958 paper; this work continued until the existence of discrete groups was proven. Further, several decades after the 1958 publication, additional errors were found in Rounsefell's analysis, such as the influence of pink salmon on sockeye salmon, the energetics of juvenile sockeye, and the relative importance of different phosphorus nutrient sources to Karluk Lake (Koenings and Burkett, 1987b; Schmidt et al., 1998). Significantly, corrections of these inaccuracies changed the paper's conclusions. For example, when errors were corrected in the phosphorus inputs to Karluk Lake, it became clear that salmon-carcass nutrients were much more important to the lake's fertility than Rounsefell had originally determined.

Rounsefell published two other scientific papers dealing with Karluk's sockeye salmon (Rounsefell, 1957, 1973). His 1957 paper on sockeye salmon fecundity was based on data collected by Rich in 1926, DeLacy in 1938–41, and Shuman in 1943. His 1973 paper responded to Van Cleve and Bevan's (1973) analysis of Karluk's sockeye salmon and defended the conclusions of his 1958 paper.

John B. Owen

1956–59

John Baxter Owen, fresh from earning his Ph.D. at Iowa State University, was hired by the BCF in late 1956 to lead the sockeye salmon research program at Karluk after Nelson was promoted to a new position in Washington, DC. Just before starting his official duties, Owen visited the research station at Karluk



John Baxter Owen (1918–). (Richard Lee Bottorff, South Lake Tahoe, CA)

[111] In 1956 Rounsefell also proposed a novel experiment to increase sockeye salmon egg production by poisoning all leeches and oligochaete worms inhabiting the spawning substrates of a Karluk tributary. These invertebrates were thought to destroy many buried salmon eggs. FWS notes (19 January 1956) on a conference with George Rounsefell. Located at NARA, Anchorage, AK.

[112] Letter (12 March 1956) from Donald L. McKernan, Administrator of Alaska Commercial Fisheries, Juneau, to Milton E. Brooding, Chairman, International North Pacific Fisheries Commission, San Francisco. Located at ABL, Auke Bay, AK.

Lake in July 1956 and helped with the last fertilization of Bare Lake. As a BCF biologist, he worked for two field seasons at Karluk (1957–58) and started several new studies of sockeye salmon.

Owen joined the BCF at a unique time in Karluk's fisheries research history. For the previous 10 years, research had focused on the possibility of fertilizing Karluk Lake to enhance its production of juvenile sockeye, and the enrichment experiment at Bare Lake was intended to test this rehabilitation idea. By 1956 Bare Lake had been fertilized for seven years and the nutrient additions had produced some positive results—the size of sockeye smolts and the smolt-to-adult ocean survivals had increased—but the abundance of returning adults seemed to have been unaffected.

Because of the positive results, considerable support still existed within the BCF to fertilize Karluk Lake. Nevertheless, by 1956 BCF officials and biologists were reviewing pre-publication copies of Rounsefell's large paper on Karluk's sockeye salmon. Rounsefell also recommended that Karluk Lake be fertilized, but at the same time he questioned the theory of declining lake fertility and discounted the potential effectiveness of any enrichment. He instead believed that predatory fishes would quickly increase in abundance and absorb any temporary benefits of fertilization. Further, he questioned if the experimental results from Bare Lake, a small shallow body of water, could be applied to a large stratified lake such as Karluk. Since no one could persuasively answer these questions, his arguments added uncertainty to the lake fertilization idea. Owen and other fishery biologists accepted the idea that fertilization may be ineffective in restoring Karluk's sockeye salmon run, and this caused them to pursue some of Rounsefell's new research ideas in the 1957 field season. Consequently, the BCF research program of 1957 included both post-fertilization studies of Bare Lake and new research ideas at Karluk Lake.

U.S. Bureau of Commercial Fisheries employees (from left) George Harry, John Owen, Ted Merrell, and Charles Conkle, Karluk Lake field laboratory, Camp Island, 1958. (Ted Merrell, Auke Bay, AK)

U.S. Bureau of Commercial Fisheries biologists Charles Conkle (left) and John Owen (right), Karluk Lake, 1957. (Auke Bay Laboratory, Auke Bay, AK)

The 1957 field season was crucially important for Owen's understanding of Karluk's sockeye salmon and the research ideas he pursued. When he first arrived at the Karluk field station, Owen knew of Rounsefell's belief that its sockeye salmon were one population, but he quickly realized that this idea was mistaken. Instead, he found that there were many distinct subpopulations, each with its own spawning time and habitat. He learned of this heterogeneity by regularly visiting the spawning areas and watching the fish segregate to specific sites as the season progressed. His assistant, Charles Y. Conkle, was instrumental in recognizing these subpopulations, having worked at Karluk since 1955 and knowing just when each sockeye run appeared at different spawning sites.

Of course, Owen and Conkle were only the latest of many previous biologists to understand that distinct run components used the spawning grounds in a repeatable sequence each year. Yet surprisingly, no one had published this evidence. If subpopulations were present, Owen began to wonder if certain spawning groups and habitats differed in their ability to produce sockeye eggs and fry. And he considered the possibility that the historic decline of Karluk's sockeye was caused by excessive commercial fishing on the most productive subpopulations.[113] Thus, much of Owen's research at Karluk focused on the productive qualities of the dif-

113 Letter (30 September 1957) from John B. Owen, FWS, Karluk Lake, AK, to W. F. Royce, FWS, Juneau, AK. Located at NARA, Anchorage, AK.

ferent sockeye salmon subpopulations and their spawning habitats.

Owen's reluctance to pursue the artificial fertilization of Karluk Lake and his disagreement with Rounsefell over sockeye subpopulations made this an uncertain and complicated time for deciding on the proper direction of the Karluk research program. Some BCF officials wanted to continue the fertilization work, but Rounsefell discouraged this. Conversely, some BCF officials discouraged subpopulation research since it conflicted with Rounsefell's belief in one population. This situation was particularly difficult for Owen, being a newly hired and untested young biologist, while Rounsefell was a respected senior scientist within the BCF.

Even with these conflicts and uncertainties, Owen managed to initiate new studies at Karluk in 1957–59, particularly on sockeye spawning habitats and their different abilities to incubate eggs and produce fry.[114] He separated the spawning habitats at Karluk Lake into four categories—lateral tributary streams, terminal tributary streams, lake beaches, and upper 5 km of the Karluk River (Owen et al., 1962). Apparently, Owen was the first biologist to use the terms "lateral" and "terminal" to distinguish the two primary types of spawning streams entering Karluk Lake. Further, he measured the areas of all sockeye salmon spawning habitats in the Karluk system and described the stream gradients and substrate compositions. Owen and his field crew regularly surveyed all of the spawning habitats in 1957–59 and documented a similar pattern of spawning use each year.

Owen also studied the distribution and behavior of sockeye salmon that spawned in several creeks at Karluk Lake in 1957–58. After adult sockeye were tagged at the lake, Owen closely monitored the movements and spawning status of these fish.[115] This study provided new information on the longevity of spawning salmon, their diurnal movements into and from spawning creeks, how quickly redds were established and eggs were deposited, and the extent of bear predation. In one instance, his field crew continuously monitored the movements and behavior of a single female sockeye salmon for three days until she spawned. Spring-run sockeye quickly established redds, spawned, and disappeared from the creeks, while later spawners had longer lives and spawning periods. The disappearance of tagged sockeye salmon varied seasonally with bear predation. Owen tried unsuccessfully to measure the total egg deposition of sockeye salmon in several creeks in 1957, but accomplished this task in 1958 with the use of FRI's egg pump. Sockeye salmon buried their eggs much deeper in terminal streams than in lateral streams. In another study, he used spawning pens to accurately assess the fate of sockeye eggs in different habitats, but this effort had limited success. [116]

Although Owen questioned the need to fertilize Karluk Lake, he nevertheless studied its limnology and several tributaries in 1958 to learn if significant declines had occurred in the nutrient levels and productivity since 1927. In fact, a few limnological changes had occurred in the 30 years, but overall most nutrient concentrations were unchanged. This apparent long-term stability in nutrients indicated to him that the lake's fertility had not declined, a conclusion that reinforced his belief that fertilization of Karluk Lake was unnecessary. The results also supported Rounsefell's skepticism of this rehabilitation idea.

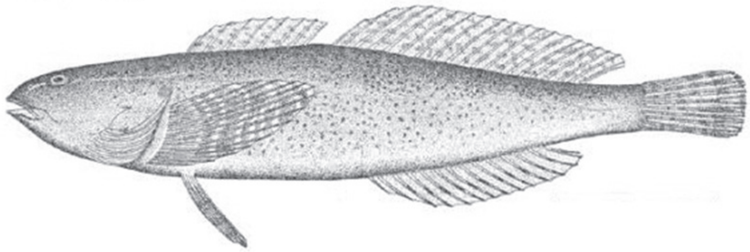
During Owen's tenure as project leader, several assistants did semi-independent studies of sockeye salmon and other fishes at Karluk Lake. For example, Conkle studied sockeye salmon fecundity in 1958 and published the results, along with similar data from Brooks Lake, Alaska (Hartman and Conkle, 1960). This paper described the relationship between female size and fecundity and noted that larger sockeye females had more eggs in the left ovary than in the right ovary. When the 1958 fecundity data were compared with earlier periods, adult female size and fecundity appeared to have experienced a long-term decline. In 1957, BCF biologist John T. Greenbank studied the life history of coastrange sculpins (Greenbank, 1957, 1966) and the food habits of Dolly Varden at Karluk Lake.[117] Since

[114] 1) Owen was greatly aided with the Karluk field studies by his two BCF assistants, Charles Y. Conkle and Robert F. Raleigh, and by many temporary personnel.
2) Owen, John B. 1958. Red salmon survival studies in Karluk Lake, Kodiak Island, 1957. Field Report. Salmon survival investigations. BCF, Alaska Region (February 18, 1958). Unpubl. report. 27 p. Located at ABL Office Files, Auke Bay, AK.

[115] 1) Letter (13 July 1957) from John B. Owen, Fishery Research Biologist, to W. F. Royce, FWS, Juneau, AK. Located at NARA, Anchorage, AK.
2) Letter (28 October 1969) from John B. Owen, Associate Professor, University of North Dakota, Grand Forks, ND, to Ben Drucker, Supervisor, Karluk Lake Research Station, Auke Bay, AK. Located at NARA, Anchorage, AK.

[116] Owen, John B. 1958. Karluk Lake weekly reports (22 June–27 September 1958). FWS, Karluk Lake, AK. 8 unpubl. reports. Located at NARA, Anchorage, AK.

[117] Greenbank, John T. 1957. Dolly Varden studies, Karluk Lake, 1957. Field Report (1 October 1957). Unpubl. report. 11 p. Located at NARA, Anchorage, AK.



Coastrange sculpin. (Drawing by Albertus H. Baldwin, from Evermann and Goldsborough, 1907.)

sculpins consumed many sockeye salmon eggs, Owen wondered if these small fishes might reduce fry production. To answer this question, he proposed a novel field experiment whereby sculpins would be excluded from a spawning creek to see if fry numbers increased, but this idea was never tested.

Each year Owen and his field crew continued with the routine tasks of collecting run composition data from sockeye adults and smolts and counting salmon through the weir. They operated the standard wooden picket weir in 1957 and a counting tower in 1958, a major new challenge for the biologists. Their attempt to measure the total smolt out-migration was unsuccessful in 1958 because of frustrating problems with the traps. Storm water and floating debris in the river damaged the traps and the smolts avoided them.

Perhaps Owen's most enduring achievement from his time at Karluk was his 1962 report that reviewed the research literature and concisely summarized the major conclusions then known about Karluk's sockeye salmon (Owen et al., 1962). He worked on this report during most of his years at Karluk and for some time afterward, preparing it for publication with co-authors Conkle and Raleigh. The report included their 1957–59 field results and discussed the possible factors that affected sockeye salmon production. They emphasized for the Karluk ecosystem the many sockeye subpopulations present, the different reproductive potentials of the many age groups, the distinct productive qualities of different spawning habitats, and the possibility that commercial fishing had altered sockeye abundance by disproportionately harvesting certain age groups and subpopulations. The BCF reviewed the manuscript for several years and eventually issued it as an ABL Manuscript Report. Though not a formal publication, the report was subsequently read, appreciated, and cited well beyond the BCF over the next 30 years, and in many respects it was functionally equivalent to a formal scientific paper. Many recent fishery biologists have stated that Owen's report was seminal to their understanding of Karluk's sockeye salmon, even though they disagreed with him on some conclusions. These positive responses demonstrated the report's long-term value.

At least four reasons explain the wide acceptance of Owen's unpublished report. First, it concisely summarized the established biological facts about Karluk's sockeye salmon. Because research had extended over many years and dealt with many complex topics, a periodic review of current knowledge is always beneficial to biologists. Second, Owen emphasized the existence of sockeye subpopulations, directly opposite to Rounsefell's idea of one population. This helped to shift the research effort in the 1960s toward finding scientific evidence of these subpopulations. Third, the report described the different types of spawning habitats in the Karluk system and how the returning sockeye used these in a similar seasonal sequence each year. Previous biologists (USBF, FWS, BCF, and FRI) also knew how returning sockeye dispersed to the spawning habitats, but Owen was the first to succinctly present this information. This repeatable spawning pattern each year was strong evidence of subpopulation differences. Fourth, the report summarized and related all of the run composition data, including sockeye salmon age, sex ratio, size, fecundity, and migration season. This large mass of salmon statistics, plus their seasonal variation, can overwhelm non-experts. Yet Owen condensed these data and interrelations into a simple table and discussed how these factors affected the sockeye salmon's reproductive potential. In summary, Owen's report provided biologists with a thoughtful and useful analysis of Karluk's sockeye salmon.

Robert F. Raleigh

1956–62

Robert Franklin Raleigh worked as a BCF fishery biologist at Karluk and Bare lakes for six field seasons in 1956–62. During this time, the research program transitioned from studying lake fertilization to researching sockeye salmon subpopulations. Raleigh spent the early part of his first field season assisting Nelson with the Bare Lake study and then temporarily led the proj-

Robert Franklin Raleigh (1926–). (Robert F. Raleigh, Saint George, UT)

ect when Nelson transferred to Washington, DC, in June 1956. After Owen joined the BCF as Karluk's research supervisor in December 1956, Raleigh assisted him in 1957–58.

Both Raleigh and Conkle proved to be particularly capable field assistants to the research leaders because of their previous field experience at Karluk and Bare lakes during 1955–58. By 1957 they knew the field operations at both lakes, often assumed responsibility for some of the studies, and provided leadership during Nelson and Owen's absence.

Raleigh temporarily left the Karluk project in mid 1957 to study the subsistence use of salmon in western Alaska (between Cape Newenham and Point Hope) and returned to the Karluk studies in 1958. Raleigh led the research program at Karluk staring in early 1959, a position he held for three years until early spring 1962.[118] He completed his B.S. (1954) and M.S. (1960) degrees at Utah State University and Ph.D. degree (1969) at the University of Idaho.

During the time that Raleigh worked at Karluk Lake, Alaska gained statehood (on 3 January 1959) and assumed full responsibility for the management of its fisheries (on 1 January 1960). Immediately, the State of Alaska made fish traps an illegal method for capturing salmon in the commercial fishery. Despite this change from federal to state authority for Alaska's fisheries, the BCF continued its long-term research program on Karluk's sockeye salmon for the next decade.

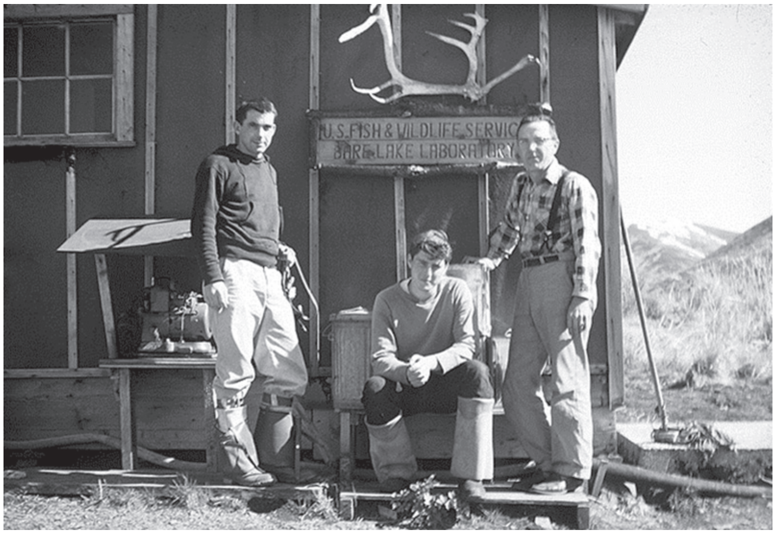
Raleigh helped Nelson complete the final fertilization of Bare Lake in 1956 and then continued post-fertilization studies on the lake until his last field season in 1961. In 1957 he studied the zooplankton of Bare Lake to learn how the previous seven years of fertilization had affected this group; he used this research for his M.S. thesis at Utah State University (Raleigh, 1960, 1963). Zooplankton abundance changed little in the first few years of fertilization, but had increased threefold by 1957. Surprisingly, the abundance of many zooplankton taxa varied with lake depth, even though Bare Lake normally was thermally unstratified. Since little post-fertilization work was done at Bare Lake in 1958, the actual number of out-migrating smolts and returning sockeye adults that year is uncertain, but smolt abundance appeared to greatly decline two years after the last fertilization. During 1959–61 Raleigh and his assistants annually collected run composition data and made detailed counts of the sockeye salmon smolts and adults. They also estimated the Dolly Varden population in Bare Lake. Following Raleigh's last field season in 1961, no further post-fertilization studies were done at Bare Lake.

Raleigh's research at Karluk was influenced by his collaborations with Owen and Conkle (Owen et al., 1962) and by Rounsefell's (1958) paper. In particular, he wanted to study two of Rounsefell's conclusions—that Karluk's sockeye run was a single population and that midseason spawners in the upper Karluk River were strays. Raleigh believed that subpopulations existed and that midseason river spawners were significant. He was opposed to fertilizing Karluk Lake because its smolts continued to be larger than those found in other river-lake systems and the Bare Lake fertilization study was incomplete.

In an early study of sockeye salmon subpopulations in 1959, Conkle and Raleigh examined the age, size, and morphology of adults at different spawning sites of Karluk Lake.[119] They found significant differences in adult size between sites; this indicated non-random use of the available habitats and the presence of subpopulations.

[118] Charles York Conkle served as Raleigh's assistant at Karluk in 1959–60, and Benson Drucker assisted in 1961.

[119] Conkle, Charles Y., and Robert F. Raleigh. 1960. Red salmon investigations. Field operations report, 1959. Sockeye salmon survival studies at Karluk Lake, Kodiak Island. BCF, Alaska Region (April 27, 1960). Unpubl. report. 20 p. Located at ABL Office Files, Auke Bay, AK.

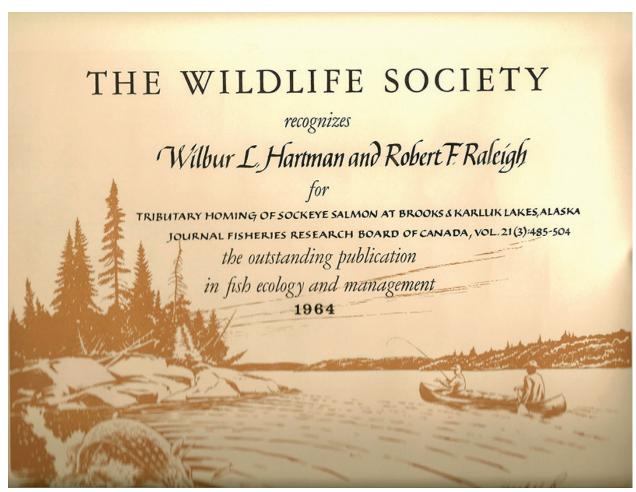


U.S. Bureau of Commerical Fisheries biologists Robert F. Raleigh (center) and Philip R. Nelson (right), Bare Lake, 1956. (Robert F. Raleigh, Saint George, UT)

Exploring the subpopulation idea further, Raleigh and BCF fishery biologist Wilbur L. Hartman conducted independent studies of tributary homing behavior by adult sockeye salmon at Karluk and Brooks lakes in 1960–61, with Raleigh doing the work at Karluk (Hartman and Raleigh, 1964). They found that rather than dispersing randomly to available spawning sites, sockeye had distinct preferences and tenaciously sought out specific lake tributaries. If blocked from entering their chosen tributary, the salmon continued to seek access until they died, rather than using an alternative spawning site. Further, when adult sockeye first entered Karluk Lake, they could not be conditioned to accept an alternative spawning creek. These impressive results confirmed that Karluk's sockeye salmon arrived at the lake spawning grounds as distinct subpopulations. Although previous biologists at Karluk had recognized the distinctiveness of spring- and fall-run sockeye, Raleigh and Hartman documented a much finer segregation that was determined by homing to specific spawning sites. The Wildlife Society honored Raleigh and Hartman for these studies, giving them their annual award for the best scientific paper in 1964.

Perhaps Raleigh's most significant research on Karluk's sockeye salmon was his innovative laboratory experiments on the migratory behavior of newly emerged fry (Raleigh, 1967, 1969). Sockeye fry from lateral and terminal streams were known to move downstream into Karluk Lake each spring, but it was less clear where the fry went that emerged in the upper Karluk River. That is, did these river fry inherently know that their nursery lake lay upstream and that they must swim against the river's current to reach the lake?

In 1958 Raleigh and Conkle arrived at Karluk Lake in early April to observe the spring fry migration. In a lateral stream, fry were absent during daylight hours, but they began migrating downstream at dusk and continued at night for about four hours. By operating upstream and downstream traps in the upper river, they discovered that fry moved slowly upstream along the riverbanks toward the lake, even in daylight, and that the entire migration lasted several weeks longer than that in lateral streams. Thus, newly emerged fry at Karluk had distinctly different responses to the direction of water flow depending on their natal site. These field observations formed the basis of Raleigh's 1965–66 laboratory experiments at the University of Idaho, where



The Wildlife Society award for outstanding publication in fish ecology and management given to Wilbur L. Hartman and Robert F. Raleigh in 1964 for their research on tributary homing of sockeye salmon at Brooks and Karluk lakes, Alaska. (Robert F. Raleigh, Saint George, UT)

Karluk River weir (center), counting huts (left), and smolt traps (right), 1957. (Robert F. Raleigh, Saint George, UT)

he tested whether the direction of fry migration had a genetic basis. In the experiments, he collected sockeye eggs from three different spawning habitats at Karluk—a lake tributary, a lake beach, and the upper Karluk River. He incubated the eggs under identical conditions at an Idaho fish hatchery. Fry produced from these Karluk eggs were placed in an artificial stream and their upstream or downstream movements recorded. Nearly all fry from lake tributaries moved downstream during the night, while most fry from the upper river moved upstream during both day and night. The different migration directions were highly significant and Raleigh concluded they were genetically determined. His experiments showed, once again, the vital importance of subpopulation differences in Karluk's sockeye salmon. He used the fry migration experiments as part of his Ph.D. dissertation at the University of Idaho (Raleigh, 1969).

Raleigh's laboratory experiments also showed that some newly emerged fry from the upper river initially moved downstream, seemingly in the wrong direction if they were to rear in the upstream nursery lake. This confusing result may be explained by Walker's studies of fry migration in the upper Karluk River during 1950–53. Walker recorded two waves of upstream fry migration in the upper river, one in the spring by smaller fry and another in late summer by larger fry.[120] This suggests that upon emerging from the river gravels, some fry proceeded directly to Karluk Lake, while others spent several months rearing in the upper river and its side sloughs before moving to the lake.

In 1962 Raleigh co-authored an important report with Owen and Conkle on Karluk's sockeye salmon, showing the existence of subpopulations that had different productive capacities (Owen et al., 1962). Raleigh later expanded on this report and prepared a new manuscript with Owen in 1969 ("Heterogeneity, homing, and selective mortality of sockeye salmon in Karluk River, Alaska") that discussed the discrete spawning subpopulations and the effects of selective fishing mortality.[121] Both reports documented that adult sockeye salmon homed to specific spawning sites at Karluk Lake in a predictable seasonal pattern each year, and that the midseason run had a higher production potential than the early and late runs. The presence of these many subpopulations suggested that commercial fishing should be spread over the entire run rather than being concentrated on the midseason, as had often occurred in the past. Unfortunately, neither of these two reports was ever formally published.

Each spring huge numbers of sockeye salmon smolts leave Karluk Lake and migrate downriver to the ocean. For many decades, biologists had wanted to accurately measure the total out-migration of smolts, but for various reasons had been frustrated by the task. Smolt out-migration was a valuable statistic to know because it integrated all of the many factors that influenced the freshwater growth and survival of juveniles. This annual output of smolts, so important to future adult returns, was also a measure of the overall productivity of Karluk Lake. Biologists experimented with different methods to measure smolt out-migration during 1954–57, but their efforts had only

[120] See footnote 99.

[121] Raleigh, Robert F., and John B. Owen. 1969. Heterogeneity, homing, and selective mortality of sockeye salmon in Karluk River, Alaska. BCF, Biological Laboratory, Seattle, WA. Unpubl. report. 25 p. Copy in personal papers of Robert F. Raleigh, Council, ID.

U.S. Bureau of Commercial Fisheries laboratory, Camp Island, Karluk Lake, ca. 1961. (Robert F. Raleigh, Saint George, UT)

U.S. Bureau of Commercial Fisheries, Auke Bay Biological Laboratory, Auke Bay, Alaska, ca. 1963. (Richard Gard, Auke Bay, AK)

gained them a relative index of abundance. Raleigh devoted much effort during his Karluk years to design a statistically reliable way to measure smolt out-migration. Though unsuccessful in 1958, he experimented with different methods in 1960 and finally succeeded in 1961 by operating smolt traps at the weir using a Latin Square statistical design. Because sockeye smolts detected slight differences in water flow, much time was devoted to observing their migratory behaviors and designing an effective trap.

Raleigh participated in many other projects at Karluk Lake, some becoming routine tasks of the research station, such as counting sockeye escapements, collecting run composition data (scales, sex, size) from sockeye adults and smolts, surveying the spawning habitats, and measuring weather data. In 1958–59 Raleigh helped build and operate the counting tower that temporarily replaced the picket weir on the upper river. Also in 1959 Raleigh used SCUBA to observe sockeye smolts migrating in the upper river and adults spawning at lake beaches.[122] He saw that the eggs of beach spawning sockeye were eaten by Arctic charr, coho salmon juveniles, and sockeye salmon grilse, but not by sticklebacks. He observed the male-female behavioral sequence that synchronized the spawning act of sockeye salmon and noted the actions of participating male grilse. Raleigh also discovered that sockeye spawning behavior differed in the lateral and terminal streams of Karluk Lake. At lateral streams, spawners entered in the morning, some dug redds and spawned, but by mid-afternoon all males and unspawned females returned to the lake for the night. Spawned females guarded their redds. At terminal streams, spawners remained there until they died. Raleigh at-

[122] BCF. 1958–1960. Monthly research report. BCF, Alaska Region. Unpubl. reports. Located at ABL Office Files, Auke Bay, AK.

tributed these two behaviors to the different vulnerabilities of spawners to nocturnal bear predation.

Besides his numerous research projects, Raleigh helped to develop the BCF research facilities on Camp Island during 1959–1961. Prefabricated materials for a new laboratory building and Pan Abode living quarters were flown by helicopter to Karluk Lake in late 1959, though these activities were interrupted when the helicopter crashed near Karluk Village. All building materials eventually reached Camp Island by late October 1959, and a work crew poured the concrete foundations before leaving for the winter. The next summer, Raleigh, Conkle, and Charles DiCostanzo, with Molly McSpadden's supervision, erected the buildings. In 1961 the new Pan Abode building was finished and the laboratory was shingled, followed in 1962 with a new 5 KW diesel power plant for electricity. In addition to the new buildings, during the 1960s some biologists and their families lived in the original cabin built on Camp Island in 1927. Raleigh renovated this old cabin in 1958 for use by his family during the field season.

During Raleigh's years at Karluk, several changes occurred in the federal management of Alaska's fisheries research. The headquarters for all federal studies of Alaska's salmon was transferred in 1956 from the Montlake Laboratory in Seattle to Juneau, Alaska. In 1960 the BCF built the Auke Bay Biological Laboratory near Juneau, and this facility served as the federal headquarters for Karluk's sockeye salmon studies until this long-term field research program ended in 1969.

Richard Gard

1962–1966

Richard Gard was the BCF project supervisor of sockeye salmon research at Karluk for four years, from July 1962 to July 1966. Previously, he had completed his Ph.D. degree at the University of California (1958) and studied Sierra Nevada trout streams; his formal training and research interests included salmonid fishes and mammalogy. Gard's field studies at Karluk focused on three research topics: the survival rates of different life stages of sockeye salmon, sockeye subpopulations, and brown bear predation on adult sockeye. He was assisted with the Karluk research by Benson Drucker, and both provided leadership to the program during 1962–66, often alternating their fieldwork at Karluk Lake and office work at the BCF's recently constructed Auke Bay Biological Laboratory near Juneau, Alaska.

Richard Gard (1928–). (Richard Gard, Auke Bay, AK)

A full program of sockeye salmon research was pursued at Karluk by the BCF during 1962–66; some studies continued those began a few years previously and others were new. The research topics on sockeye salmon included fry migrations, lake residence of juveniles, timing and abundance of smolt out-migration, travel times of adult migration, adult escapements to individual tributaries, fecundity, egg deposition, brown bear predation, and limnology of Karluk Lake (Fig. 2–3). Routine tasks included the weir installation and operation, sockeye escapement counts, collection of run composition data, stream surveys, and weather records.

Many years before Gard began to study the survival rates of different life stages of Karluk's sockeye salmon, fishery biologists had fully understood the importance of this research topic. If biologists could determine when the greatest mortality occurred in the life cycle, it then might be possible to isolate specific factors that had caused the declining sockeye runs. Barnaby (1944), after documenting remarkably high marine survival rates for Karluk's sockeye salmon, shifted his studies to the freshwater life stages. Yet, previous attempts to measure the freshwater survival were unsatisfactory because of unsolved research problems with

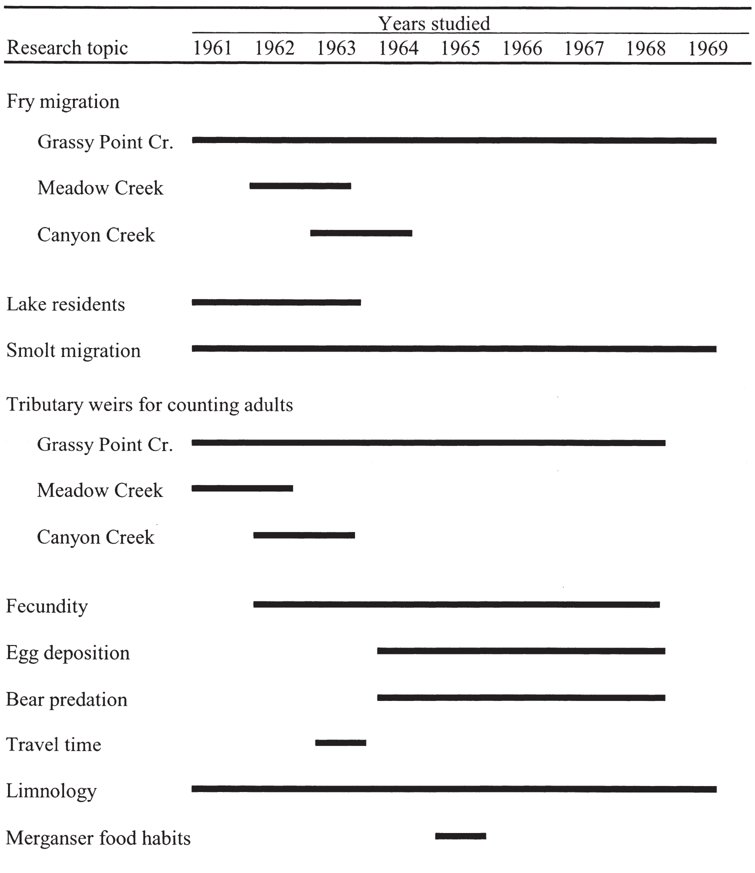


Figure 2-3. Karluk sockeye salmon research, 1961–69.

field gear and sampling methodology. Fortunately, when Gard began his studies in 1962, four important advances in field gear and methods had just been made: 1) accessory weirs to accurately count the adult sockeye that entered specific spawning streams, 2) an egg pumping device to measure egg densities in stream substrates, 3) traps in tributary streams to precisely count emerging fry, and 4) traps in the Karluk River weir and a statistically valid design to measure total smolt out-migration.

Using these new field improvements, along with data on sockeye salmon fecundity, abundance, and run composition, Gard obtained the freshwater survival rates at several lateral and terminal streams at Karluk Lake. Specifically, he determined the number of eggs brought into a stream by the adult females (potential egg deposition), live and dead eggs buried in the substrate at the end of the spawning season (actual egg deposition), live eggs in the substrate (egg survival in September–October), and fry produced the following spring and summer (over-wintering survival). Only 10–15% of eggs brought into the stream survived as live eggs at the end of the spawning season, but 30–40% of those survived through the winter and produced fry. Most egg mortality occurred during the spawning act, and losses decreased once eggs were buried in the stream gravels. Egg mortality during spawning was caused by eggs retained in females, eggs washed away before they were buried in the substrate, superimposition of spawning redds, and bear predation on spawning females. Egg-to-fry survival rates were greater in terminal streams than in lateral streams. Total freshwater survival (potential egg deposition to smolt produced) was typically less than 0.5%. Marine survival (smolt-to-adult) was 30–50%, much higher even than Barnaby (1944) reported, but similar to Ricker's (1962) estimates. Since freshwater survival rates at Karluk were lower than in many other sockeye salmon systems, Gard concluded that "some factor(s) in the freshwater environment must be important in maintaining the low level of the run" (Gard and Drucker, 1966b). Thus, these studies were noteworthy in obtaining, for the first time, accurate survival data on several freshwater life stages and additional measurements of the marine stage.

Gard devoted considerable effort during 1962–65 to gathering field evidence of sockeye salmon subpopulations, especially after Rounsefell (1958) discounted their presence. Gard collected morphological and behavioral data at different sites and seasons at Karluk, looking for discrete sockeye salmon groups. Stream

Karluk Lake and Camp Island (near), looking toward Thumb River valley, 1966. (Richard Gard, Auke Bay, AK)

surveys showed that adult sockeye returned to different spawning habitats in a repeatable seasonal pattern each year, and these differences were evident in lateral and terminal streams, lake beaches, and the upper river. Likewise, significant site and seasonal differences occurred in fry and adult sizes, ages, and fecundity. Female size and fecundity differences showed that reproductive potential varied by spawning site and for spring- and fall-run fish.[123] Gard concluded that Karluk's sockeye salmon had at least two major subpopulations and that each principal spawning habitat likely had its own discrete group (Gard et al., 1987).

Gard measured the travel time of fall-run adult sockeye salmon between the Karluk River Portage and upper weir (14 km) in 1963 and compared his results with the 1945–46 unpublished tagging study of Shuman and Nelson (Gard, 1973). Spring-run sockeye ascended the entire river in about 7 days, while fall-run fish needed about 10 days. As the spawning season progressed and the fish approached sexual maturity, travel times declined for both spring and fall runs.

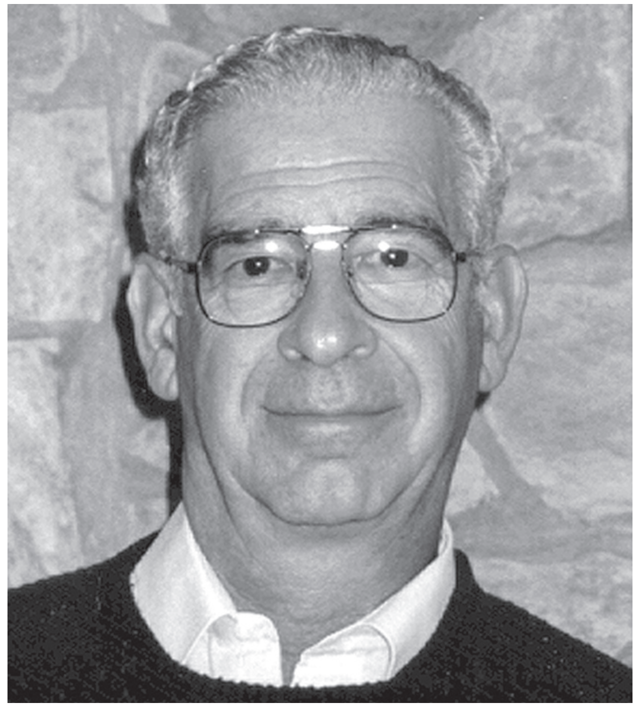
Gard studied brown bear predation on sockeye salmon at Grassy Point Creek, a lateral tributary of Karluk Lake, in 1964–65. In both years he counted the number of adult sockeye that entered the creek, salmon carcasses, and bear-killed salmon and their spawning status. Bears had free access to the creek in 1964 and killed many salmon, though most fish had spawned before dying. An electric fence partially excluded bears from the creek in 1965, greatly reducing the number of bear-killed salmon. Gard (1971) concluded that bear predation had little effect on the overall production of sockeye salmon in Grassy Point Creek.

[123] Most of this fecundity data remained unpublished, though some was published (Gard et al., 1987) or presented in ABL Manuscript Reports.

Karluk Lake and Five Fingers Mountain, viewed from Camp Island, 1965. (Richard Gard, Auke Bay, AK)

Most of Gard's sockeye research data during 1962–66 were presented in five ABL Manuscript Reports, one for each field season (Gard and Drucker, 1963, 1965, 1966a, b; Drucker and Gard, 1967). Though never formally published, these reports were distributed to several fisheries libraries and were of great interest to other salmon biologists because they contained scientific information about little-known aspects of sockeye biology. For example, using downstream fish traps placed in Karluk's tributaries, Gard recorded the number and timing of newly emerged sockeye fry in the spring migration. Significantly, the pattern of fry migration closely matched that of the adult spawners from the previous year. Similarly, regular smolt collections documented the seasonal out-migration of sockeye and coho salmon, including their diurnal movements, lengths, weights, and ages. These reports also summarized data on the sockeye escapements, weir operation dates, run composition, and stream surveys. Limnological and climatological data were regularly collected at Karluk Lake during 1962–66, but none were included in these reports.

Gard briefly studied the food habits of mergansers (*Mergus merganser* and *M. serrator*) at Karluk Lake and the upper river in June 1965. Of 18 individuals examined, seven from the lake had eaten sticklebacks. Five mergansers from the O'Malley and upper Karluk rivers had eaten salmonid fry or smolts and some were sockeye salmon. One merganser collected at the Karluk River near Silver Salmon Creek had eaten 43 salmonid fry.



Benson Drucker (1931–2000). (Benson Drucker, Reston, VA)

Benson Drucker

1961–70

Benson Drucker worked as a BCF fishery biologist at Karluk for nine field seasons during 1961–70. He assisted Raleigh in 1961 and Gard in 1962–1966 before leading the Karluk studies in 1966–1970. Drucker was hired by the BCF in December 1960 after completing his M.S. degree at the University of Miami. The BCF research program underwent dramatic changes during his years at Karluk, including an expansion of the facilities on Camp Island in the early 1960s and then a complete end of all field studies in 1969. This period was also notable for the transition of responsibilities from the BCF to the ADFG for the fisheries research and management of Karluk's sockeye salmon. Though Drucker's last field season at Karluk was 1969, he continued to analyze his research data through 1970 before leaving Alaska in May 1971.

Drucker participated in most of the field studies of sockeye salmon while assisting Raleigh and Gard during 1961–66 and, in fact, led some projects. Sockeye salmon research then comprised fry migrations in tributary streams, egg survival and fry production of different spawning sites, distribution of juveniles in Karluk Lake, tributary homing of adults, evidence of sockeye subpopulations, bear predation on adult sockeye, smolt out-migrations, and post-fertilization monitoring of Bare Lake. Drucker also helped with the routine annual tasks of installing and maintaining the Karluk River weir, counting escapements, collecting run composition data of sockeye adults and smolts, surveying spawning streams, and gathering limnological and climatological data.

Drucker helped to determine the total out-migration of sockeye smolts from Karluk Lake during his first field season in 1961. This was the first statistically accurate measurement of smolt out-migration, while all previous attempts since 1954 only had given a relative abundance index. To do this, traps were built into the weir and operated in a statistical design to obtain the smolt abundance for that year. The ability to measure smolt production was a significant achievement for the Karluk research program since it now allowed the freshwater and marine survival rates of sockeye salmon to be known. Operation of the weir traps each spring also gave the biologists accurate data on the timing and composition of the smolt migration.

Pumping stream substrate for sockeye salmon eggs, Karluk Lake tributary, 1966. (Benson Drucker, Reston, VA)

Sockeye salmon fry migration nets, Grassy Point Creek, 1963. (Benson Drucker, Reston, VA)

Transporting adult sockeye salmon to Halfway Creek, Karluk Lake, 1968. (Benson Drucker, Reston, VA)

Drucker studied the juvenile sockeye of Karluk Lake in 1961–62 as part of a much larger investigation of many sockeye salmon systems in southwestern Alaska by the BCF, FRI, and ADFG (Burgner et al., 1969). For the first time, the fishes of Karluk Lake were collected with littoral beach seines and limnetic tow nets; both sampling methods were needed to understand the distribution of juvenile sockeye in the lake. Ellis (1963) published some of the data on fish distribution and abundance in Karluk Lake, and Drucker prepared another report around 1965 with additional information.[124] Though his report was never published, some of the data were later used in a comparative study of salmon nursery lakes (Burgner et al., 1969).

Continuing work started in the early 1960s, Drucker investigated the sockeye salmon spawner abundance, egg survival, and fry production of Grassy Point Creek during 1967–69. Each year he measured the number of sockeye spawners that entered the creek, the egg density in the substrate, and the number of fry produced the following spring. Again, most of the egg mortality occurred during the spawning process, but once eggs were entrained in the substrate mortality was low. Fry production was negatively correlated with the number of spawning females that entered the creek (at least for the range of 2500–5700 females).

To further examine the fry-spawner relationship, Drucker (1968, 1970) experimentally reduced the number of spawners allowed to enter the creek in 1967–68. Lower spawning densities increased initial egg survival, but winter egg survival and fry production decreased, possibly because too few adults were present to adequately clean the spawning gravels. The adult sockeye salmon that were prevented from entering Grassy Point Creek were transported 3 km south and released into Halfway Creek, where a weir kept them from returning to their home stream. Higher spawning densities in Halfway Creek increased the egg retention of transferred females, but these alien fish eventually spawned among themselves and with native sockeye.

In 1968 Drucker recorded unusually low egg survival (3%) between those brought into Grassy Point Creek in female bodies and those found in the gravel after spawning ended. In previous years he had found much higher egg survivals (12–23%) and attributed the huge loss of eggs in 1968 to bear predation on the sockeye spawners. Reportedly, 97% of the recovered female carcasses had been killed by bears.

Drucker prepared a report on this bear predation in 1970 and compared the alarming 1968 data with that of 1966–67. His report was revised several times over the next few years and given a new title but was never published.[125] Drucker claimed that spring-run sockeye in small lateral creeks were most vulnerable to bear predation, while later spawners in larger terminal streams and lake beaches were in less danger. This conclusion matched previous observations that spring-run fish quickly spawned after entering lateral creeks (Conkle, Raleigh, and Owen, 1959).[126] After considering all the facts, Drucker concluded that bear predation had little overall effect on sockeye salmon abundance at Karluk, but was intense at specific times and places.

Drucker co-authored several formal scientific papers on Karluk's sockeye salmon. First, he described the migratory behaviors of fry and smolts at Karluk and compared these with other river-lake systems in Alaska and British Columbia (Hartman, Heard, and Drucker, 1967). The data for this paper were collected at Karluk during 1961–64, the first time that both fry and smolt migrations had been accurately measured. His study included underwater observations of migrating fish in Karluk Lake and River. The paper gave information on the seasonal timing of fry and smolt migrations, diel variations of migrations, environmental factors initiating migrations, schooling behavior, depth and orientation of fish to stream currents, and fry and smolt predators.[127] Years later, Drucker co-authored a formal paper with Gard on the sockeye salmon subpopulations at Karluk, documenting the differences in adult size and age, fecundity, spawning habitat, and fry migration and

[124] Drucker, Benson. ca. 1965. Age, size, abundance and distribution of juvenile sockeye salmon (*Oncorhynchus nerka*) at Karluk Lake, Alaska, 1961–1962 (Original title: "Juvenile sockeye salmon resident studies at Karluk Lake, Kodiak, Alaska, 1961–1962"). BCF, ABL, Auke Bay, AK. Unpubl. report. 30 p. Located at NARA, Anchorage, AK.

[125] Drucker, Benson. 1973. Determining the effect of bear predation on spawning sockeye salmon on the basis of rate of disappearance of tagged salmon. (Original 1970 Title: "Extreme bear predation on sockeye salmon spawners at Grassy Point Creek, Karluk Lake, Kodiak, Alaska"). BCF, ABL, Auke Bay, AK. Unpubl. report. 54 p. Copy in the personal papers of Richard Gard, Juneau, AK.

[126] Owen, John B. 1958. Red salmon survival studies in Karluk Lake, Kodiak Island, 1957. Field Report. Salmon survival investigations. BCF, Alaska Region (February 18, 1958). Unpubl. report. 27 p. Located at ABL Office Files, Auke Bay, AK.

[127] It is of historical interest that this paper was selected for the 1968 "Charles Y. Conkle Annual Publications Award" from the BCF Auke Bay Biological Laboratory, AK. This annual award was initiated to honor BCF Fishery Biologist, Charles York Conkle, who worked as a young biologist at Karluk Lake during 1955–60. Conkle's promising career as a fishery biologist was prematurely ended by a fatal illness.

U.S. Bureau of Commercial Fisheries research facilities, Camp Island, Karluk Lake, 1977. (Auke Bay Laboratory, Auke Bay, AK)

size (Gard et al., 1987). This paper, in addition to several others from this era, finally settled the question about the existence of sockeye salmon subpopulations in the Karluk run (Owen et al., 1962; Hartman and Raleigh, 1964; Raleigh, 1967; Wilmot and Burger, 1985). In addition to these formal publications, Drucker wrote many ABL Manuscript Reports that summarized the sockeye salmon data collected each year from Karluk during 1962–68 (Drucker, 1968, 1970; Drucker and Gard, 1967; Gard and Drucker 1963, 1965, 1966a, b). He also compiled a bibliography of published and unpublished studies done at Karluk and Bare lakes (Drucker, 1971).

Besides his sockeye salmon research, Drucker studied the life history of coho salmon at Karluk during 1961–68, gathering data on the adults and smolts, ages, sizes, fecundity, eggs, and seasonal and diel migrations (Drucker, 1972). Karluk's juvenile coho salmon, similar to its sockeye, resided longer in freshwater than reported for other river systems, and adults had high fecundities (4,700 eggs per female). The coho smolt migration peaked about 1–2 weeks after that of sockeye smolts.

During Drucker's nine field seasons at Karluk Lake, the BCF research facilities at Camp Island were greatly enhanced. Improvements included new living quarters, research laboratory, storage sheds, boathouse, and boats. Personnel and supplies reached the lake via agency aircraft (Grumman Goose) or chartered flights. A diesel power plant and generator supplied electricity to the buildings, and reliable radios provided direct communication between the biologists and managers around Kodiak Island.

Nevertheless, federal funding for salmon research at Karluk became increasingly scarce in the 1960s. These fiscal constraints led Drucker to request in October 1966 that the ADFG assume responsibility for the Karluk River weir and collection of run composition and smolt out-migration data. To conserve funds in 1967–69, the BCF hired fewer temporary workers for the field studies.[128] In contrast to the BCF's situation, federal funding to the ADFG increased after passage of the Anadromous Fish Act. Consequently, beginning in 1967 the ADFG operated the Karluk River weir and collected the run composition data, while the BCF installed the weir and measured the smolt out-migration. The BCF ended all field research on Karluk's sockeye salmon on 15 July 1969; in that year they restricted their studies to the fry migration at Grassy Point Creek, smolt out-migration, and limnological sampling. Measurement of the spring 1969 fry migration was more difficult than normal because winter-like conditions persisted and the lake was still ice-covered in April, making it difficult to reach the creek. Drucker and his assistant, Ray Sautter, reached Camp Island in early April on a Kodiak Airways Bell 206 turbine helicopter.[129]

Drucker experienced several curious events during his many field seasons at Karluk. For example, when extra funds became available in 1961 to study several sockeye systems in southwestern Alaska, the BCF purchased three new boats for the Karluk research program. The boats (two dories and a cabin cruiser) were delivered to Karluk Village on the lower river in July

[128] Beyond the funding shortages, the BCF found it difficult to hire temporary workers in 1968 because of the Vietnam War. Typically, college students were hired for these summer jobs, but in early 1968 some students were reluctant to leave school for fear of being drafted.

[129] The BCF rarely used helicopters for transport to Karluk Lake.

1961, and Drucker and his assistant, Darrell Farmen, physically pulled the boats 40 km upriver to Karluk Lake, a grueling task because the river was especially low that year. Their feat is the first record of a full ascent of the Karluk River while hauling a boat and supplies, though many biologists had brought boats 14 km upriver between the Portage and lake. Drucker and his assistant, James Romero, also brought a new Boston Whaler boat upriver to Karluk Lake in 1967, but this time they started at the Portage.[130]

On another occasion, King Mahendra and Queen Ratna of Nepal used the BCF research station on Camp Island as their base camp for an 8-day bear hunt in November 1967. These facilities normally accommodated 6–8 people, but the royal hunting party and supporting personnel totaled 35, causing Drucker to add several improvements (room heaters, walkways, and insulated toilet). As part of a wider big-game safari in Alaska, the royal party shot a bear at Karluk Lake.[131]

Finally, Drucker helped the crew members of Jacques Cousteau's vessel *Calypso* film a movie about sockeye salmon at Karluk Lake in August 1969. The movie crew photographed sockeye salmon and brown bears and filmed an interview with Drucker. The movie, *Tragedy of the Red Salmon,* later won an award at the Cannes Film Festival in France.

[130] Over the many years that boats (often loaded with supplies) were pushed and pulled up the Karluk River, at least one person died from this strenuous effort. In the spring of 1963, bear hunting guide Griska Nikolai, then age 53, suffered a heart attack as he pushed a boat up the O'Malley River (Dodge, 2004).

[131] Apparently, the King shot a bear in an area recently closed to hunting. The area had been closed because of concern that bear harvests at Karluk Lake were excessive (Van Daele, 2003). A description of the King and Queen's visit to Alaska, their bear hunt at Karluk Lake, and the subsequent controversy has been written from the viewpoint of Al Burnett, head guide (Connelly, 1969).

CHAPTER 3

Karluk River Weir

At last! Accurate counts of spawning salmon.

For the first 39 years of commercial fishing on Karluk River sockeye salmon (1882–1920), federal managers responsible for regulating the fishery and assuring that adequate numbers of fish reached the spawning grounds were at a severe disadvantage. From the fishery's earliest years, they knew the number of salmon being harvested and packed at nearby canneries, but they did not know how many were spawning in and near Karluk Lake. Managers tried to regulate this fishery without knowing how many sockeye salmon actually escaped the fishery. They understood that adequate numbers of fish must spawn each year to perpetuate future runs, but they lacked a definite measure of the yearly reproduction. Even rough estimates were lacking because direct observations of spawning sockeye salmon at Karluk Lake were rare before 1919. Estimates of escapement numbers were further complicated during 1896–1916 because sockeye that eluded the commercial fishery then migrated through Karluk Lagoon where many were taken for hatchery brood stock.

Although officials and employees of the early canneries also realized that sufficient numbers of sockeye salmon must spawn each year, apparently no one tried to estimate the numbers that migrated upstream. Only rarely is it noted in the historical Karluk literature that cannery personnel visited Karluk Lake to see the sockeye's spawning grounds, though company officials often worried that the then-abundant salmon runs might decline. Most likely, some visits did occur in the early years, but these were uncommon events and produced no gauge of spawning escapements. Instead, cannery personnel focused their attention and energy on the sockeye salmon harvests at the lower Karluk River and ocean waters off Karluk Spit, not on the spawning grounds at Karluk Lake:

> The men at the head of the canneries know the cannery business thoroughly. They know how to get the fish to the canneries, pack them, case them for market, and figure on the profits, but it is exceptionally rare to find one who had followed even his home stream to its source and examined the lake system and the spawning grounds. . . . The cannerymen are in the country for fish and not for investigation or scientific research. (Moser, 1899)

Ingwald Loe, APA hatchery superintendent in 1910, visited Karluk Lake several times, possibly to evaluate it for a new hatchery site. He incorrectly claimed that "fully two thirds of the salmon spawn in the lake itself, chiefly along the northeastern shore. . . the lake feeders do not carry many spawning fish, not being big enough or of suitable bottom."[1] Likewise, Moser, then an APA official, briefly reached Karluk Lake's outlet during this same period, but not having a boat, he explored no further (U.S. Senate, 1912). Perhaps one possible reason why cannery officials generally lacked an intense interest in the spawning grounds at Karluk Lake was their firm belief that the modern hatchery on Karluk Lagoon, which operated from 1896 to 1916 and released millions of fry, would be a major support to future runs of sockeye salmon.

Federal regulations on fishing times, places, and gear were enacted in the early years of Karluk's fishery, but these laws were based on qualitative judgments of what might allow sufficient numbers of fish to escape the fishery. Often, in practice, the regulations were poorly enforced or the fishermen and canneries ignored or found ways around them. Typically, the fishing and cannery operations were unmonitored for nearly the entire season, the government inspector usually visiting Karluk's canneries for one day each year. Canneries operated under self-imposed fishing rules in some early years, and rival companies closely monitored each other's actions for compliance. Moser (1899) declared in 1897 that "the laws and regulations pertaining to Alaska salmon fisheries are very generally disregarded, and that

[1] Fassett, H. C. 1910. Report on the salmon hatchery operated by the Alaska Packers Association on Karluk Lagoon, Kadiak Island, Alaska. Unpubl. report. 25 p. Located at Alaska Historical Collections, Alaska State Library, Juneau.

they do not prevent the illegal capture of fish." Yet federal regulatory officials apparently believed that sockeye salmon escapements to Karluk Lake were adequate prior to 1921 because laws restrained the harvest and fishery inefficiencies allowed sufficient fish to enter the river.

But the once-famous runs of Karluk River sockeye salmon had greatly declined by 1920, and it was obvious that the number of fish reaching the spawning grounds must be accurately known in order to scientifically manage this resource. This conclusion was reached, in particular, by the renowned fishery biologist Charles H. Gilbert of Stanford University, along with several USBF officials, including Henry O'Malley, Field Agent; Ward Bower, Chief Agent of the Alaska Fisheries Service; and Hugh Smith, Commissioner of Fisheries. To accurately measure the number of sockeye migrating to the spawning grounds, they installed a salmon counting weir across the Karluk River in 1921 and operated it between May and October. By collecting these weir data for a number of years, they reasoned that a definite relationship would be found between the known escapements and subsequent numbers of returning sockeye salmon. If such a correlation could be established, management of the fishery would be easier and sockeye runs would be placed on a sustainable basis.

For many centuries Karluk's indigenous Alutiiq people had placed wooden and stone barriers across the river to impede and concentrate the migrating salmon for easy capture. The Russians also used similar barricades on Alaska's rivers in the 1800s to help them harvest salmon to provision their sea otter hunting crews. During his reconnaissance of Karluk Lake and River in 1889, Bean (1891) observed and photographed a line of boulders placed across the upper river to concentrate migrating salmon. Remnants of these early barriers continued to be visible at several locations on the Karluk River into at least the 1960s. Salmon counting weirs outwardly resemble some of these early river barriers, except that weirs have several narrow openings where fish are counted as they pass by and continue to the spawning grounds.

Ever since the first Karluk salmon counting weir was erected in 1921, federal, state, and private entities have continually discussed and reevaluated its location, design, and operation (Tables 3-1 and 3-2; Fig. 1-4). Changes to the weir since 1921 reflect the shifting balance between management, research, and conservation viewpoints. In this chapter, we review the history of the Karluk River weir and its continued importance as a research and management tool for sockeye salmon and other salmonid fishes.

Table 3-1

Karluk River weir operations, 1921–2010.

Year	Location	Agency	In charge	Date installed	Date removed	Operational problems[1]
1921	Lagoon	USBF	Fred R. Lucas	26-May	26-Oct.	1, 2, 4, 6, 7
1922	Lagoon	USBF	Fred R. Lucas	12-May	25-Oct.	1, 2, 4, 5, 6, 7
1923	Lagoon	USBF	Ray S. Wood	21-May	12-Oct.	2, 4, 5
1924	Lagoon	USBF	Ray S. Wood	14-May	21-Aug.	1
1925	Lagoon	USBF	Ray S. Wood	18-May	6-Oct.	2, 6
1926	Lagoon	USBF	Ray S. Wood	14-May	14-Oct.	2
1926	Portage	USBF	Harley W. Barton	2-June	11-Sept.	
1927	Lagoon	USBF	Ray S. Wood	12-May	13-Oct.	7
1928	Lagoon	USBF	Ray S. Wood	10-May	13-Oct.	2, 4, 6
1929	Lagoon	USBF	Ray S. Wood	10-May	14-Oct.	
1930	Lagoon	USBF	Ray S. Wood	17-May	9-Oct.	
1931	Lagoon	USBF	Ray S. Wood	14-May	8-Oct.	2, 6
1932	Lagoon	USBF	Harry D. Baer, H. Olafson	13-May	4-Oct.	1
1933	Lagoon	USBF	Charles P. Turner	14-May	9-Oct.	
1934	Lagoon	USBF	Morris Rafn	22-May	5-Oct.	1, 2
1935	Lagoon	USBF	Howard H. Hungerford	11-May	5-Oct.	2, 4
1936	Lagoon	USBF	James O'Brien	11-May	7-Oct.	1
1937	Lagoon	USBF	James O'Brien	17-May	6-Oct.	
1938	Lagoon	USBF	James O'Brien	13-Apr.	3-Sept.	1, 2
1939	Lagoon	USBF	James O'Brien	19-May	22-Sept.	2
1940	Lagoon	FWS	James O'Brien	19-May	25-Aug.	1
1941	Lagoon	FWS	Allan C. DeLacy	23-May	8-Sept.	
1942	Portage	FWS	Joseph Corkill	9-May	15-Oct.	2, 3
1943	Portage	FWS	Richard F. Shuman	31-May	9-Sept.	2, 3, 4
1944	Portage	FWS	Richard F. Shuman	25-May	31-Aug.	1, 2, 3
1945	Lake Outlet	FWS	Richard F. Shuman	29-May	10-Oct.	1
1946	Lake Outlet	FWS	Richard F. Shuman	3-June	20-Oct.	2, 4

Table 3-1 (cont.)
Karluk River weir operations, 1921–2010.

Year	Location	Agency	In charge	Date installed	Date removed	Operational problems[1]
1947	Lake Outlet	FWS	Richard F. Shuman	26-May	3-Oct.	
1948	Lake Outlet	FWS	Richard F. Shuman	20-May	3-Oct.	1
1949	Lake Outlet	FWS	Richard F. Shuman	22-May	28-Sept.	
1950	Lake Outlet	FWS	Philip R. Nelson	20-May	9-Oct.	
1951	Lake Outlet	FWS	Philip R. Nelson	27-May	13-Oct.	
1952	Lake Outlet	FWS	Philip R. Nelson	25-May	7-Oct.	
1953	Lake Outlet	FWS	Philip R. Nelson	18-May	2-Oct.	
1954	Lake Outlet	FWS	Philip R. Nelson	20-May	1-Oct.	
1955	Lake Outlet	FWS	Philip R. Nelson	13-May	4-Oct.	
1956	Lake Outlet	FWS	Philip R. Nelson	20-May	6-Oct.	
1957	Lake Outlet	BCF	John B. Owen	15-May	3-Oct.	
1958	Lake Outlet Tower	BCF	John B. Owen	31-May	1-Oct.	
1959	Lake Outlet Tower	BCF	John B. Owen	31-May	7-Oct.	
1960	Lake Outlet	BCF, ADFG	Robert F. Raleigh	29-May	10-Oct.	
1961	Lake Outlet	BCF, ADFG	Robert F. Raleigh	22-May	3-Oct.	
1962	Lake Outlet	BCF, ADFG	Richard Gard	14-May	29-Sept.	
1963	Lake Outlet	BCF, ADFG	Richard Gard	20-May	28-Oct.	
1964	Lake Outlet	BCF, ADFG	Richard Gard	17-May	17-Oct.	
1965	Lake Outlet	BCF, ADFG	Richard Gard	15-May	2-Oct.	
1966	Lake Outlet	BCF, ADFG	R. Gard, B. Drucker	18-May	22-Sept.	2
1967	Lake Outlet	ADFG		17-May	28-Sept.	
1968	Lake Outlet	ADFG		13-May	7-Oct.	
1969	Lake Outlet	ADFG		23-May	12-Oct.	2, 7
1970	Lake Outlet	ADFG		27-May	12-Oct.	
1971	Lake Outlet	ADFG	Thomas A. Emerson	13-June	12-Oct.	
1972	Lake Outlet	ADFG	Thomas A. Emerson	31-May	28-Sept.	
1973	Lake Outlet	ADFG	Greg Moore	8-June	10-Oct.	
1974	Lake Outlet	ADFG	Rod Neterer	31-May	10-Oct.	
1975	Lake Outlet	ADFG	Rod Neterer	3-June	2-Oct.	
1975	Lagoon Tower	ADFG	Robert Tomaselli			
1976	Lagoon	ADFG	Harry Dodge	23-May	17-Sept.	1, 2
1977	Lagoon	ADFG	Len Schwarz, Ken Langlois	21-May	8-Oct.	2
1978	Lagoon	ADFG	Herman Savikko	19-May	23-Oct.	1, 2
1979	Lagoon	ADFG	Mark Willette	13-May	5-Oct.	
1980	Lagoon	ADFG	Charles Burkey, Jr.	26-May	10-Sept.	1
1981	Lagoon	ADFG	Tim Perry	29-May	23-Sept.	
1982	Lagoon	ADFG	Steve Brown	20-May	15-Sept.	1
1983	Lagoon	ADFG		15-May	25-Sept.	
1984	Lagoon	ADFG	Matt Cole	22-May	29-Sept.	1
1985	Lagoon	ADFG		23-May	26-Sept.	
1986	Lagoon	ADFG		21-May	2-Oct.	
1987	Lagoon	ADFG		20-May	29-Sept.	
1988	Lagoon	ADFG		25-May	17-Sept.	
1989	Lagoon	ADFG		22-May	16-Sept.	
1990	Lagoon	ADFG		29-May	8-Sept.	
1991	Lagoon	ADFG		26-May	23-Sept.	
1992	Lagoon	ADFG	Ed Sampson III	25-May	26-Sept.	
1993	Lagoon	ADFG	Mike Brase	24-May	29-Sept.	
1994	Lagoon	ADFG		9-May	23-Sept.	
1995	Lagoon	ADFG	Michael Anderson	20-May	24-Sept.	
1996	Lagoon	ADFG	Michael Anderson	24-May	25-Sept.	1, 2
1997	Lagoon	ADFG		19-May	25-Sept.	
1998	Lagoon	ADFG		21-May	26-Sept.	2
1999	Lagoon	ADFG		26-May	23-Sept.	
2000	Lagoon	ADFG		25-May	24-Sept.	8
2001	Lagoon	ADFG		24-May	18-Sept.	
2002	Lagoon	ADFG		23-May	28-Sept.	
2003	Lagoon	ADFG		17-May	28-Sept.	2, 8
2004	Lagoon	ADFG		22-May	6-Oct.	1, 8
2005	Lagoon	ADFG		27-May	24-Sept.	2, 8
2006	Lagoon	ADFG		21-May	20-Sept.	
2007	Lagoon	ADFG		20-May	26-Sept.	
2008	Lagoon	ADFG		23-May	22-Sept.	2
2009	Lagoon	ADFG		23-May	29-Sept.	
2010	Lagoon	ADFG		23-May	19-Sept.	

[1] 1 = salmon carasses, 2 = high water, 3 = aquatic weeds, 4 = debris, 5 = high tide, 6 = muddy water, 7 = ice, 8 = bear damage to weir.

Table 3-2

Biological advantages and disadvantages of the three weir locations on the Karluk River.

Weir on the Lower Karluk River near Lagoon

Advantages

1) Sockeye salmon counts are more complete because they include those spawning in Karluk Lake, its tributary streams, and upper Karluk River. Small numbers of sockeye spawning below the weir in Karluk Lagoon must be added to the counts.
2) Sockeye salmon counts are obtained closer to the commercial fishery, allowing for better management decisions. Weir tenders can periodically survey Karluk Lagoon to estimate the numbers of salmon that have passed the commercial fishery, but have yet to pass the weir.
3) Sockeye scales collected close to the ocean are in better condition for reading ages.
4) Counts of other salmon species are more complete—pink (July–August), Chinook (May–July), coho (August–September), and chum.
5) Counts of up-migrating steelhead (September–October) and down-migrating kelts (May–June) are more complete.

Disadvantages

1) Pink salmon carcasses that drift downstream in even-numbered years often threaten to washout the weir in August–September.
2) Steelhead kelts must efficiently pass the weir in May–June or suffer increased mortality.

Weir at Karluk River Portage

Advantages

1) Sockeye salmon counts are more complete because they include those spawning in Karluk Lake and its tributary streams and in the upper Karluk River.
2) Pink salmon carcasses that drift downstream seldom threaten the weir.

Disadvantages

1) Masses of aquatic plants growing just upstream in the Karluk River drift against the weir in late summer, requiring regular cleaning to prevent its washout.
2) The weir is further removed from the commercial fishery, giving longer travel times for up-migrating sockeye and making management decisions more difficult.
3) Pink salmon counts are incomplete because much spawning occurs in the river downstream.
4) Steelhead kelts must efficiently pass the weir in May–June or suffer increased mortality.

Weir near Karluk Lake's Outlet

Advantages

1) Pink salmon carcasses and aquatic weeds seldom threaten the weir's integrity.

Disadvantages

1) The count of fall-run sockeye salmon is less complete because some fish spawn in the Karluk River below the weir and their numbers must be estimated.
2) The weir is further removed from the commercial fishery, giving longer travel times for up-migrating sockeye and making management decisions more difficult.
3) Sockeye salmon scales collected further from the ocean are more difficult to age.
4) Counts of pink, Chinook, coho, and chum salmon are incomplete because most of these fish spawn in the Karluk River below the weir.
5) Steelhead counts are incomplete because most winter in the Karluk River downstream from the weir. Kelt counts are incomplete.

Weir near Karluk Lagoon (1921–41)

1921

The USBF installed a wooden picket weir across the Karluk River in the summer of 1921 and counted the sockeye salmon migrating upstream. This, Alaska's first salmon-counting weir, was located on the lower Karluk River a short distance upstream of Karluk Lagoon and 5 km from the ocean at Karluk Spit. A total of $500 was appropriated for the weir and cabin, the weir lumber alone costing $400. The 93 m weir had three counting gates, one in mid river and one near each riverbank. Fred Lucas, USBF fish culturist at Afognak hatchery, installed and operated the Karluk weir in 1921, under the general supervision of Gilbert:

> [Speaking of the Karluk River weir, 1921] A site for the rack was decided upon just above the head of the lagoon. This spot was chosen principally because it was just out of reach of the tides, a comparatively smooth and level gravel bottom, as narrow a place as could be found within a mile and to facilitate the transportation of material as this had to be carried or dragged up the river proper by main strength and ackwardness.
>
> For the foundation of the rack, we used three legged "horses" . . . They were constructed of poles about ten inches in diameter, the two down stream legs seven feet long and the upstream leg nine feet long. These horses were spaced ten feet apart, then two stringers (also poles) were nailed on parallel with the water line. The pickets, (1½″ × 1½″ sawed lumber) were then nailed on at right angles to the stringers and spaced close enough so the fish could not get through.
>
> The material and tools necessary for building the barrier, left Kodiak on the gas boat "America", April 25th and picked up a tow of poles for the frame work at Whale Island near Afognak.
>
> Everything was discharged safely at the mouth of the Karluk River next day. The material was rafted and floated up the lagoon, then dragged up the river to the rack site. Living quarters were established in the old

hatchery, property of the Alaska Packers Association, about one half mile below.

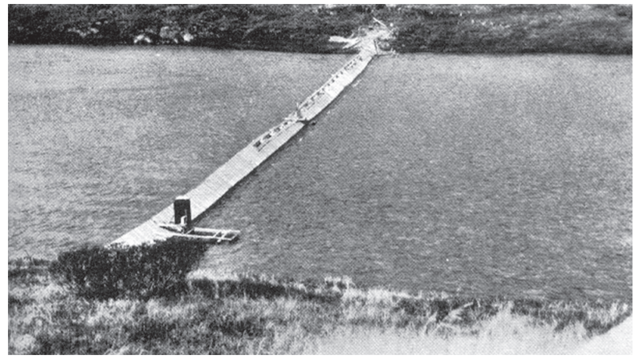
The vents were constructed so they could readily be adjusted to any desired width enabling us to let the fish through only as fast as they could be easily tallied. A cloudy sky or muddy water will sometimes slow the work down, often preventing all the fish at the barrier getting through before dark. A piece of white canvas laid flat on the river bottom and arranged so the fish must swim over it, helps greatly.[2]

Weir operations and fish counting proceeded without unexpected major problems for most of 1921, and for the first time, accurate counts of adult sockeye reaching the spawning grounds were obtained. Without a doubt, the counting weir on the Karluk River proved to be feasible to operate and valuable for the data collected.

William Baumann, USBF warden at Afognak, operated the weir in the final weeks of the 1921 season (19 Sept.–3 Nov.) and described several weather-related problems with maintaining the weir into late October:

[Speaking of the Karluk River weir, late 1921] You will notice that no fish were tallied September the 30th and October the 6th. Those days were after the heavy rains which caused so much trouble by bringing down large quantities of debris, such as dead fish, turf grass and some small brush, which kept us cleaning rack all day. Anyway the river was too rily to see the fish. Just before these floods the fish would come to the rack in great numbers, most of the counting was done in the afternoon. Preparations were made October 27th to take up the barrier as the temperatures were falling rapidly. And October 28 started to take off pickets as drift ice was coming down, also anchor ice was forming. The water raised nearly to the top of rack and the rack had the appearance of a worm fence and some of the horses slipped back two or three feet owing to the heavy pressure. Ice had to be knocked off of pickets and horses before taking them to the river bank. Two horses were left in River, as Mr. Lucas and myself thought it would be a good idea. It might help determine the force of the ice.

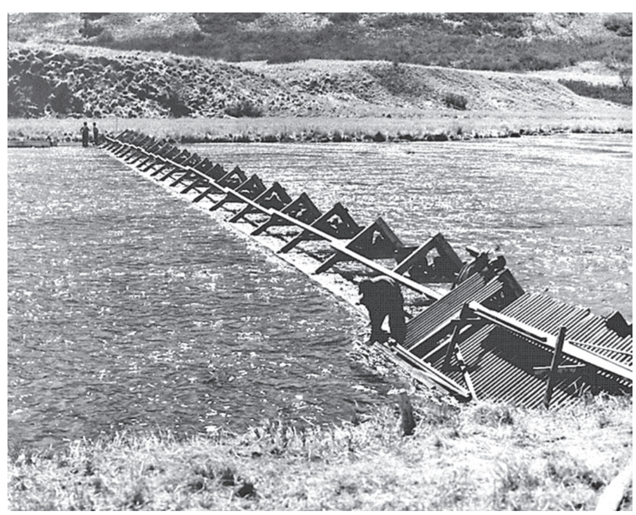
November 2 packed up all paraphernalia and started for Karluk. Had to break ice along the shore of lagoon to get dories out as lagoon was frozen over about one third distance.[3]



First Karluk River salmon counting weir, on lower river just upstream of Karluk Lagoon, 1921. (From Bower, 1922)

The materials and methods used to install, operate, and remove the Karluk River weir have remained nearly the same since 1921. Typically each year, the weir was installed in May and removed in September or October, all weir parts and lumber being stored on the riverbank for the winter because of the ice-covered river. The weir was usually constructed directly across the river at a right angle to the riverbanks and current, though an angled weir was tried during a few years.

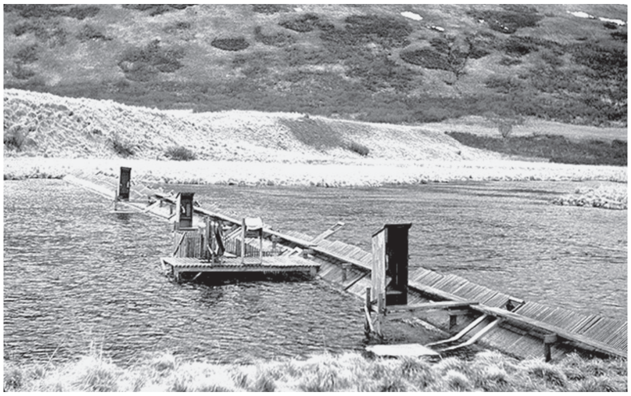
To install the weir, large tripods (known as "horses") made of stout poles or timbers were placed in a straight line across the river, spaced about 3 m apart, and positioned with one tripod leg facing upstream and two legs facing downstream. Rocks from the river were placed on the tripods to add weight and stability to resist the river's force. Next, two rows of wooden stringers were nailed to the upstream legs of adjacent horses and parallel to the water surface, one stringer



Installing the Karluk River weir, near Karluk Lake's outlet, 18 May 1949. (Auke Bay Laboratory, Auke Bay, AK, FWS-1125)

[2] Lucas, Fred R. 1922. Report of the census of red salmon that escaped to the Karluk Lake spawning grounds during the season of 1921. U.S. Dep. Commer. Bur. Fish. Unpubl. report. 14 p. Located at NARA, Anchorage, AK.

[3] Letter (10 November 1921) from W. E. Baumann, Afognak, AK, to Henry O'Malley, Seattle, WA. Located at NARA, Anchorage, AK.



Karluk River salmon counting weir, near Karluk Lake's outlet, 20 May 1954. (Clark S. Thompson, Shelton, WA)

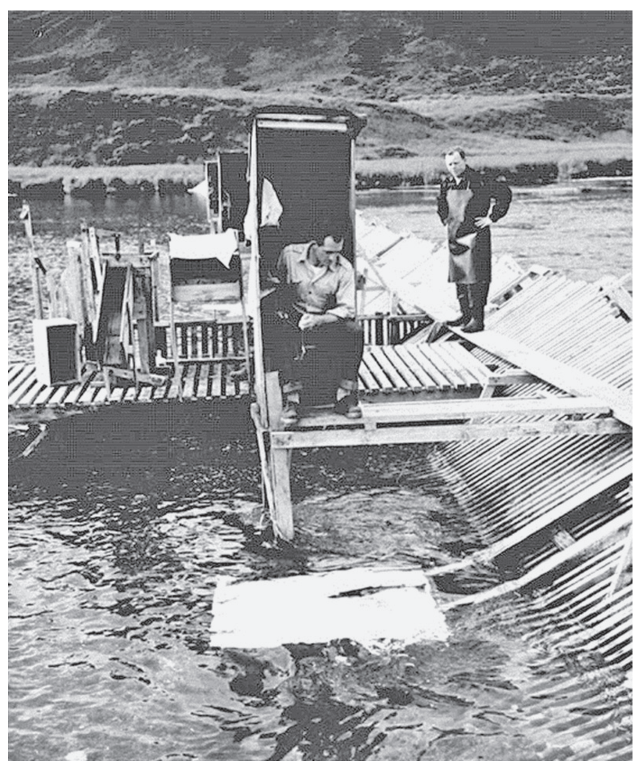
positioned near the water surface and the other located nearer the top of the horses.

Wooden pickets were then attached perpendicularly to the stringers, with one end against the river substrate and the opposite end near the top of the horses. Pickets were narrowly spaced to prevent fish passage but still allow the river to flow through the weir. Pickets were placed at the same inclined angle as the upstream leg of the horses, and by their continuous placement across the river they formed a barrier to upstream salmon movements, except at several counting gates. Wooden pickets (3.8 × 3.8 cm) were used for many years, each being nailed to the stringers, but in recent years, aluminum rods joined into panel units have been used.

Three or more counting gates were built into the continuous wall of pickets. With counting gates closed, the weir formed a complete barrier to upstream salmon migration. Depending on the number of salmon ascending the river, one or more gates were opened and the fish were counted through the weir. Workers had access along the entire weir by a horizontal catwalk plank, sometimes with safety handrails. Common features added to the basic weir were gates, traps, and pens for catching adult salmon; smolt traps; and various platforms to help workers collect scales and measure fish lengths and weights. Because the crew worked in all types of weather, including strong winds and heavy rains, small houses were sometimes built over the counting gates to give partial shelter. White cloth or panels placed on the river bottom just upstream of each counting gate gave a contrasting background to help identify and count passing fish.

Although biologists primarily installed the 1921 Karluk weir to count migrating adult sockeyes, they also learned much more about sockeye salmon biology, seasonal migrations of other fish species, and the river ecosystem. Diligent weir operation required several workers to devote constant daily attention to river conditions, weather, and fish movements from May to October. The daily duties of counting fish upstream, maintaining the weir, recording water temperatures, and living next to the river provided a sustained series of biological observations from one location. Such regular observations thus resulted, somewhat unexpectedly, in much greater knowledge about the river and its biota. In particular, the dynamic nature of its fish migrations became known for the first time, including the upstream and downstream migrations of adults and juveniles of all five salmon species, Dolly Varden, and steelhead trout. Further, the biologists observed the interactions between salmon and various birds (bald eagles, gulls, terns, and mergansers) and mammals (brown bears, river otters, and red foxes).

Typical of most new attempts at field research, operating the 1921 Karluk weir revealed unexpected biological features. Immediately after installing the barrier, many Dolly Varden began accumulating above the weir, becoming so numerous that they interfered with salmon counting. The weir barred the annual down-migration of Dolly Varden to the ocean each spring, these fish being very thin and in poor condition follow-



Counting sockeye salmon as they come through the Karluk River weir, September 1948. (E. P. Haddon, Auke Bay Laboratory, Auke Bay, AK, FWS-1223)

ing winter. Next, the weir crew observed the down-migration of sockeye smolts in early June, but poor collecting gear kept them from getting specimens for Gilbert to study. Spawned-out steelhead (kelts) also accumulated above the weir in June and the crew modified the weir to let them pass downstream. Dolly Varden began their up-migration from the ocean in July, and in stark contrast to the down-migrants, these fish were in excellent condition. As the season progressed, the up-migrations of Chinook, pink, and chum salmon were noted, followed by coho salmon and steelhead in the autumn. Regular samples of sockeye salmon scales were lacking in 1921, except for two incidental collections from 211 fish in August.

Once the counting weir began successful operation on the Karluk River in 1921, fishery biologists and managers immediately expanded its use beyond the primary purpose of counting sockeye salmon. The weir quickly became an important research and management tool, a value that continues to present times.

1922

Based on the 1921 operations, Lucas recommended that the 1922 weir be installed at an angle across the river, reasoning that this position would concentrate down-migrating Dolly Varden and steelhead kelts at the lower end, where they could be easily trapped or released. Up-migrating sockeye supposedly would concentrate at the upper end of the weir, where several counting gates would be located. Consequently, the 1922 weir was installed at a 50° angle across the river, with two counting gates at the upper end. Being angled, additional lumber was needed to construct the 110 m weir. Additional counting gates were later built into the weir near its middle and lower end. After operating the 1922 angled weir, Lucas concluded it had no advantages in speeding the up-migration of salmon.

The 1922 weir had several additional purposes besides counting sockeye salmon, perhaps the most important being the collection of adult sockeye scales from throughout the whole run. From more than 2,000 scales collected in 1922, Gilbert determined the age composition of the Karluk sockeye run. Because of their scientific value, salmon scales have been taken at the weir nearly every year since 1922. Another new function of the 1922 weir was to capture and destroy thousands of migrating Dolly Varden; these fishes were believed to be serious predators of sockeye eggs and juveniles. Destroying these charr was part of an ongoing predator control program by governmental agencies and commercial interests.

In contrast to the relatively trouble-free weir operations of 1921, more difficulties occurred with the 1922 weir because of the pink salmon run which, at Karluk, varies greatly in abundance between even- and odd-numbered years. Runs are usually small in odd years and large in even years. As the 1922 weir season began, Lucas and his weir crew realized that the pink salmon run might be larger than in 1921, but they were mainly concerned whether they could simultaneously distinguish and count both sockeye and pink salmon as they swam through the open gates. In fact, about 400,000 pink salmon entered the river from mid July to mid August 1922, and the crew found it impossible to accurately count the pink salmon on days of large migration.

Nevertheless, these counting errors were the least of their problems as pink salmon passed through the weir gates, spawned in the river upstream, and then died. By 10 August salmon carcasses began to drift downstream and accumulate against the weir. The crew made a valiant effort to clean the weir and keep it functional, spending many hours throwing carcasses over the weir. Rainstorms raised the river on 20 August, flushing masses of decomposing carcasses against the weir faster than they could be removed. An estimated 50,000 carcasses accumulated against the weir on 21 August, plugging it and causing the river to overtop and undermine the structure. To save the weir from complete washout and destruction, sections of pickets were removed to pass the carcasses downstream. But these open weir sections allowed uncounted sockeye salmon to move upstream from 20 August to 4 September, causing inaccuracies in the 1922 escapement data.

The 1922 season dramatically illustrated the main problem of operating a weir on the lower Karluk River—the risk of weir washout from masses of even-year pink salmon carcasses. From 1922 to present times, pink salmon carcasses have caused problems for weir crews. Tarleton Bean (1889), the first biologist to investigate Karluk's fisheries, commented on the pink salmon carcasses from the huge 1880 run:

> [At Karluk River, 1880] At the end of the run the humpbacks began dying, and those that did not get up to Karluk Lake were floating down dead or dying for one month. The banks of the stream were strewn with dead fish, and the stench was more easily imagined than endured.

Perhaps it was fortunate that the first Karluk River weir operated in an odd-numbered year when the new weir crew could focus on counting sockeye and not have to contend with pink salmon carcasses. One wonders if the weir program would have continued if the

first attempt had been in an even year when pink salmon carcasses destroyed the structure. In 1922 Lucas and his crew lived at the abandoned APA hatchery, located about 0.8 km downstream from the weir.

1923

Compared with the previous year's problems, the 1923 weir operation ran rather smoothly. Ray Wood, a USBF employee at the Afognak Fisheries Station, installed and operated the weir. Four counting gates were used to give salmon rapid upstream passage. He closely observed the migratory behavior of adult sockeye, finding that they first gathered for several days in a deep hole at the upper end of Karluk Lagoon and then proceeded upstream to the weir as a group. Salmon arrived at the weir in pulses, there being several days with few fish, followed by several days with many fish. He noted that adult salmon migrated at night and wondered if counting hours might be extended by installing lights on the weir. Wood observed the spring down-migration of sockeye smolts and measured the length of a few fish (100–200 mm). The spring down-migration of Dolly Varden seemed smaller than usual, but the up-migration was large, at times outnumbering the sockeye salmon. The crew installed weir traps to capture and destroy Dolly Varden, but failed to collect sockeye salmon scales in 1923.

An unusually high tide, in combination with strong winds and a storm-swollen river, overtopped and undermined the weir on 12 October, letting some sockeye pass upstream uncounted. Grass, aquatic weeds, and debris drifted against the weir and plugged it; the increased water pressure pushed the weir a few feet downstream and broke some pickets. Shortly thereafter conditions improved and the crew safely removed the structure, storing it on the riverbank for winter.

After operating the Karluk weir for three years and gaining critical fisheries data, there was no doubt of its value and that the program would continue. Nevertheless, following the 1923 weir season and continuing for the next four years, considerable discussion, controversy, and indecision occurred over its proper location on the Karluk River. These events apparently were triggered by a 1923 letter from A. K. Tichenor, APA Vice President and General Superintendent, to Henry O'Malley, Commissioner of Fisheries, criticizing the location of the lower Karluk River weir.[4] Tichenor declared that the weir harmfully impeded the salmon's ascent of the river. He argued that swift currents at the weir exhausted many salmon before they found open gates, causing them to give up their migration, drift downstream, and either die or spawn unnaturally in the lower river or Karluk Lagoon. As evidence, he alleged that carcasses of exhausted salmon often lined the riverbanks below the weir and that salmon disfigured from repeated attempts to pass the weir had been caught off Karluk Spit. Tichenor suggested that the weir be moved upstream to Karluk River Portage, reasoning that the deep slow current there would let salmon rest while waiting to pass the weir. He recommended a V-shaped weir built with netting or wire mesh and felt that the Portage site was superior because it had good access from Larsen Bay.

Tichenor's criticisms of the existing weir site apparently came from information he received in 1923 from Gordon Jones, then serving his first year as APA Superintendent at Larsen Bay cannery. Jones visited the Karluk River weir once on 10 June 1923 when sockeye were present, but no salmon carcasses then lined the banks. Since salmon carcasses only littered the lower river following the even-year pink salmon runs, it appears that Jones's knowledge of the weir came from his one visit, plus previous observations made by others who confused pink salmon carcasses with those of sockeyes. Assertions that the weir exhausted salmon and caused them to drift downstream to spawn in Karluk Lagoon also lacked credibility. Typically, only a few hundred or thousand sockeye spawned in Karluk Lagoon each year, perhaps a natural remnant of the millions of hatchery fry released during 1896–1916. As biologists now realize, salmon are not easily deterred from their spawning migration; they tenaciously pursue their natal spawning grounds.

Both Lucas and O'Malley responded to Tichenor's criticisms, discounting his claim that the weir harmed the sockeye salmon. Direct observations of the salmon's migratory behavior by Lucas and Wood during 1921–23 failed to support the criticisms. O'Malley cautioned Tichenor that moving the weir further upstream may reduce cannery harvests because escapement counts would not include salmon present in the river below the weir. Nevertheless, he accepted the possibility of moving the weir to the Portage, provided the canneries contributed to the costs. Tichenor offered APA's assistance in establishing a new weir, agreeing to transport weir materials from San Francisco to the head of Larsen Bay on company vessels. He also offered to supply a horse and sled to transport

[4] Letter (17 October 1923) from A. K. Tichenor, Vice-President and General Superintendent, APA, San Francisco, CA, to Henry O'Malley, U.S. Fish Commissioner, Washington, DC. Located at NARA, Anchorage, AK.

the materials from Larsen Bay to the Karluk River Portage and agreed that the 4 km trail needed improvements across marshy areas.

Once the possibility existed in late 1923 of moving the weir's location, lengthy discussions ensued within the USBF and canneries about its best site on the Karluk River. Three locations were advocated: 1) the present site on the lower river upstream of Karluk Lagoon, 2) the Portage, and 3) the upper river near Karluk Lake's outlet. Arguments for or against a particular site focused on research, management, and practical concerns (Table 3-2). These discussions continued over the next four years, often with proponents of particular sites changing their preferences.

The main problem at the lower weir site was the threat of washout every two years from pink salmon carcasses, this causing inaccurate sockeye salmon counts. At the Portage site, carcasses would be less of a problem, but Lucas warned of a possible difficulty with that location. Growing immediately upstream of the Portage were dense beds of aquatic plants that decayed each autumn and drifted downstream, again potentially plugging the weir and threatening its washout. Lucas considered Tichenor's suggestion of a web weir at the Portage impractical because of the aquatic plant problem and stated that a typical wooden weir was better at that site. If a web weir must be used, Lucas suggested a fourth site in upper Karluk Lagoon, the nets crossing on pilings from the old hatchery to just upstream of a deep hole on the north bank.

Some biologists and officials believed the best weir site was at Karluk Lake's outlet. Pink salmon carcasses and aquatic vegetation would seldom be problems there, but, unfortunately, weir counts would be inaccurate because many thousands of fall-run sockeyes spawned in the Karluk River below the proposed site. The abundance of these river spawners may not have been well known when the alternative weir sites were being considered. Inaccessibility, poor communications, and remoteness from the commercial fishery also made this a poor site for the fishery managers and canneries. Reconciling sockeye salmon escapements and commercial catches would be more difficult because of fish that had escaped the fishery and were ascending the river, but not yet counted at the weir. For practical reasons, Lucas believed a web weir could be successfully operated at Karluk Lake's outlet.

1924

As the 1924 weir season approached and debate continued over the proper location, it soon became evident for logistical reasons alone that no change could be made for the upcoming season. Gilbert and O'Malley decided to keep the 1924 weir on the lower Karluk River, but adjusted its location slightly to secure it against pink salmon carcasses. A 107 m angled weir with six counting gates was installed on the lower river in 1924. Although an angled weir in 1922 had failed to speed salmon migration, this design was used again in 1924 with the idea that it would help move pink salmon carcasses downstream by floating them along the weir face to an opening at the lower end.

Notable as these preparations were, they proved to be futile because over 4,000,000 pink salmon flooded into the Karluk River in 1924. To let the hordes of upmigrating pink salmon quickly pass the weir, all six counting gates were opened. Since complete counts of sockeye salmon were impossible with the two-man crew, they estimated the escapement by proportionally expanding the accurate counts made at one or two gates to the four or five open uncounted gates. At the manned gates, they accurately counted sockeye, but only estimated pink salmon. Lucas commented on the large numbers of salmon at the 1924 weir:

> [At Karluk River weir, 1924] The river was so full of fish behind the rack that there was danger of them smothering, or otherwise hurting themselves, if held until they could be counted through by the two men.[5]

This huge salmon run, combined with low flow conditions in mid summer, overwhelmed the oxygen capacity of the Karluk River and caused a large fish kill for 16 km above the weir. All fish species in the river were killed, including adult sockeye, pink, and Chinook salmon, Dolly Varden, steelhead, and juvenile salmonids:

> [At Karluk River weir, 1924] After they passed through the weir quite a number died before spawning for a distance of at least ten miles above the weir. The cause for this is not known for certain, but owing to the fact that salmon fingerlings, adult red salmon and trout in the area also died and floated down the stream it is believed that there were too many fish for the oxygen content of the water, especially as there seemed to be a slight fall of the water level at the same time.[6]

Many pink salmon carcasses, plus those from the fish kill, began accumulating against the weir and threatened to overwhelm it by 22 August. To save the

[5] Letter (30 December 1924) from Fred R. Lucas, Superintendent, Clackamas, OR, to Commissioner of Fisheries, Washington, DC. Located at NARA, Anchorage, AK.
[6] See footnote 5.

weir from complete washout, the crew removed many pickets and stopped counting sockeye salmon. They unsuccessfully tried to reestablish the weir and resume counting in late August and September, but pink salmon carcasses continued to be such a problem that the 1924 weir season ended two months earlier than normal and well before the sockeye run had ended.

Following passage of the federal White Act in 1924, the Karluk River weir became an important tool for management of its sockeye salmon runs. This law mandated that 50% of the total salmon run must be allowed to escape to the spawning grounds, a proportion assumed to be sufficient to sustain this resource. By matching ongoing counts from the weir with harvest data, managers could now accurately determine if the 50% mandate was being met and, if not, they could close the fishery.

1925

The 1925 weir was again installed on the lower Karluk River and operated without major problems. Gilbert visited the weir in May–June to collect sockeye smolts and scales from down-migrating Dolly Varden. The weir crew used three fish traps to capture and destroy Dolly Varden. They tested a fish wheel at the weir, but it was unsuccessful. They installed wire leads below each counting gate to guide and speed the upstream passage of adult sockeye, but these additions also proved unsuccessful. In late May, workers captured a "candlefish" (either *Ammodytes hexapterus* or *Thaleichthys pacificus*) at the weir, a rarity in the lower river.[7] Gilbert tagged 200 adult sockeye in early August and measured their travel time between Karluk Spit and the weir. Weir tenders saw sockeye salmon spawning in upper Karluk Lagoon and noted the presence of gill-net marked salmon. Heavy rains in early October raised the river, making counting difficult in the turbid waters.

By mid 1925 the USBF had decided to locate the 1926 weir near Karluk Lake's outlet to avoid the problem of salmon carcasses. After the 1924 ordeal, pink salmon carcasses were expected to be a problem in the lower river in 1926. To solve the problem of the lake's remoteness, O'Malley initially wanted a telephone line installed between Karluk Spit and Karluk Lake, but later he tried to procure wireless telephones.

APA vessels delivered a large load of lumber to the western end of Larsen Bay in 1925, near the ocean end of the Portage trail. This lumber was intended for a new weir and cabin or tent frame shelter at Karluk Lake in 1926. USBF warden Howard Hungerford was responsible for transporting the lumber, coal, and other supplies to the lake. To accomplish this task, a Fordson track-laying tractor was moved from Afognak Fisheries Station to Larsen Bay in late 1925.

The original plan called for hauling the materials to Karluk Lake with the tractor and sled during the winter of 1925–26, when a deep snow pack capable of supporting heavy loads normally covered the unstable muskeg. Hauling began in January 1926, but mild weather and lack of snow prevented direct hauling to Karluk Lake. By mid January Hungerford had moved the materials 1.2 km to the ridge above Larsen Bay by hauling small loads across temporarily frozen ground in early morning hours. Continuing this work, he hauled six tractor loads to the Karluk River Portage and then about 2 km upstream, where he unloaded it on the riverbank, still 12 km from Karluk Lake. This hauling occurred without the benefit of snow cover, the tractor pulling the loaded sled across rough frozen muskeg.

At this point the tractor broke down and repairs consumed the next two weeks. When hauling resumed in early February, the tractor badly mired in muskeg on its first trip across the Portage trail and required two days to extract. As the time remaining for winter snows and cold temperatures diminished, Hungerford realized he was unlikely to get the weir materials to the lake. Nevertheless, by mid February as the weather turned milder, he had hauled another four loads to the

USBF biologist Arnie J. Suomela driving Fordson tractor across the Karluk River portage trail, 1934. (Joseph Thomas Barnaby, from Lynn L. Gabriel, Herndon, VA)

[7] In 1903 Cloudsley L. Rutter reported that in the Karluk region "candlefish" were the sand launce, *Ammodytes alascanus,* now a synonym of *A. hexapterus.* Cloudsley L. Rutter memo notebook for 1903 (16 June–14 July), Karluk Spit, Portage, River, and Lake. Located in Box 130, Barton Warren Evermann papers, Library Special Collections, California Academy of Sciences, San Francisco, CA. Also see Chamberlain (1907).

supply cache on the riverbank. He made no further attempts to haul materials by tractor and sled, or to get weir materials to Karluk Lake, even though 8–10 additional loads remained on the ridge above Larsen Bay. Hungerford concluded that enough lumber existed at the Karluk River supply cache for a 122 m weir, which could be constructed at the Portage site in 1926. O'Malley still wanted the 1926 weir at the lake's outlet, but if that was impossible, to again install it on the lower river, not at the Portage. He suggested that Hungerford move the materials by skiff up the Karluk River in spring, but that was not done.

1926

Failure to transport the new weir materials to Karluk Lake's outlet in the winter of 1925–26 renewed the discussions of where it should be located, and a decision was urgently needed since the weir season rapidly approached. With 1924 in mind, biologists feared the 1926 pink salmon run would be so large that these fish might enter the spawning streams at Karluk Lake and damage eggs already deposited there by sockeye. Thus, one reason for choosing the lake weir site was to prevent pink salmon from entering the sockeye's spawning grounds. Though a wooden picket weir at the lake's outlet was impossible in 1926, O'Malley decided in mid April to place a weir on the lower Karluk River and a heavy web weir at the lake's outlet as a barrier to pink salmon. The cotton webbing could be procured and installed at the lake's outlet prior to the early August pink salmon run but not in time to count the June sockeye run.

These 1926 weir arrangements were unsatisfactory to Gilbert, who wanted two weirs in place to insure accurate counts of sockeye escapements, even if pink salmon carcasses rendered the lower weir inoperable late in the season. Also, two weirs would let him measure the travel times of sockeye migrating between Karluk Spit and Karluk Lake.[8] Finally, Gilbert, Hungerford, and Rich conferred at Larsen Bay on 25 May and decided that their only real alternative for a second weir in 1926 would be at the Portage site. Consequently, two Karluk River weirs operated in 1926, one on the lower river and another at the Portage. In 1926, the weir crews lodged in the abandoned hatchery at the lower river and in a new cabin at the Portage.

Rich spent considerable time in early 1926 at the lower Karluk River weir marking sockeye smolts and watching adults ascend the river, especially noting their behavior at finding and passing through the counting gates. Aware of past criticisms by the canneries, he decided their arguments against the weir had little merit:

> [At Karluk River weir, 1–2 June 1926] It was obvious that the weir formed no serious obstacle to the ascent of the fish as they easily found the openings.
>
> It is certainly an imposing sight to see them coming on up stream in large shoals, splashing over the shallow riffles in almost solid masses. They are especially numerous just below the rack where they are, nightly, slightly delayed. It is very evident, however, that the delay occasioned by the rack is by no means serious. The fish run lively for a time and then drop back in more quiet water below—possibly into the lag[oon]—and then come on up again later. There is no evidence that the fish are in any way injured by the delay. They lie quietly behind the rack, working along until they come to an opening through which they can pass. It has been claimed that the rack works a real injury to the run but now I can observe the conditions as they are here today and really believe that there is nothing to such a claim.[9]

Unexpectedly, over 2,500,000 sockeye salmon escaped to the Karluk River in 1926. The Portage weir had hardly been installed in early June when large numbers of sockeye accumulated downstream. Fearing the fish might smother, the crew opened all weir gates and removed sections of pickets on 10–11 June, allowing free upstream passage to about 350,000 sockeye. Operating two weirs in 1926 allowed the travel times of adult sockeye to be measured over the 20 km separating the two sites. Of 100 fish tagged at the lower weir on 19 July, they passed the Portage weir on 21–28 July.

Contrary to all expectations, the 1926 pink salmon run was small and salmon carcasses never threatened to wash out either weir. Pink salmon never reached the lake spawning grounds or damaged sockeye redds. When the large pink salmon run failed to appear by mid September, counting operations were ended at the Portage weir. The webbing material purchased to exclude pink salmon from the lake went unused.

As the 1926 weir season drew to a close, discussions began anew about the proper weir location for 1927.[10] The consensus weir site in September 1926 was Karluk Lake's outlet. Gilbert requested that O'Malley make an early decision so materials could be

[8] Letter (24 May 1926) from J. R. Russell, Field Superintendent, USBF, Seattle, WA, to Henry O'Malley, USBF, Washington, DC. Located at NARA, Anchorage, AK.

[9] Rich, Willis H. 1926 notebook. Location of original notebook unknown; copies at NARA, Anchorage, AK, and ABL Library, Auke Bay, AK.

[10] Discussions were between Henry O'Malley, Charles H. Gilbert, and several USBF personnel (Willis Rich, Howard Hungerford, Dennis Winn, and J. R. Russell).

transported well before the next weir season.[11] Yet, when Hungerford reported on the 1926 weir operations in October, he recommended that the best weir location was the lower river, not the Portage or lake's outlet:

> [Concerning the 1927 Karluk River weir location] It is recommended that this weir be maintained at its present location during coming years to secure an early and accurate count of salmon entering Karluk river. The prejudice under which this weir has labored is entirely a thing of the past and everyone interested in the conservation of salmon is convinced that its location is the logical one.[12]

Nevertheless, in December 1926, Hungerford, Gilbert, and Rich agreed that the 1927 weir should be located at the Portage, but they also wanted additional weir lumber transported and stored at the lake's outlet. This would give them the option of locating future weirs at any of three sites.[13] In February 1927 O'Malley and Dennis Winn preferred the site on the lower river, but sought further opinions from Gilbert and Rich. Gilbert agreed that the lower site had advantages for management purposes, there being fewer uncounted fish in the river, but in March Rich continued to prefer the Portage site. Finally, O'Malley decided that the 1927 weir would be on the lower river. This decision settled the question of the proper weir location for the next 15 years, without further discussions by USBF personnel or criticisms from the canneries.

1927

Although the 1927 location had been decided, when it came time to install the weir, some confusion arose about its design. A V-shaped weir with its apex pointing downstream had been planned to help Rich collect, mark, and census sockeye smolts. But the person installing the weir was unaware of the new design and he, instead, built a normal straight weir. A late breakup of the river ice delayed weir installation several weeks in 1927; the river banks and upper lagoon had large ice packs on 1 May. Once operating, the 1927 weir season proceeded without major problems.[14] Weir removal in late October proved to be difficult because anchor ice plugged the weir and caused a partial washout. Living quarters in 1927 were found in a room of the old hatchery building and in a woodshed. A small weir cabin was built in the summer of 1927 using lumber salvaged from the abandoned APA hatchery.

Rich continued to believe the best weir site was the lake's outlet and wanted to convince O'Malley and Gilbert to make the move in 1928. As Rich marked sockeye smolts at the lower weir in 1927, drifting algae and debris clogged his wire mesh traps, confounding efforts to capture and count these migrants. He believed smolt traps could be operated at the lake's outlet, plus it appeared to be a good location to capture Dolly Varden and count adult sockeye. Further, 1928 seemed to be a good time for moving the weir because existing materials at the lower river were worn and needed replacing. To lessen the difficulty of transporting lumber to the new site, Rich had planned on building the weir horses from cottonwood logs cut at the lake. He hoped to get a final decision on the 1928 weir from O'Malley and Gilbert so materials could be moved to the lake in the summer of 1927.

1928–41

Notwithstanding Rich's desire for a new weir site in 1928, it continued to be operated on the lower Karluk River during 1928–41. By 1927 the original weir lumber from 1921 was deteriorating and new living quarters were needed for the crew. The old hatchery building, once used by the weir crew for shelter, was completely gone by 1929, its lumber and parts having been scavenged for other uses. Thus, the USBF delivered new weir lumber to Karluk in 1929 for use in 1930. A small cabin was built at the weir in 1929 and another in 1932; the APA listed the two cabins in a 1933 inventory of their Karluk properties, though they charged the USBF no rent.

During this period, weir operation became a routine annual USBF duty. The weir was typically installed in mid May and removed in early October. Weir crews counted sockeye salmon and collected salmon scales

[11] Letter (27 September 1926) from Charles H. Gilbert, USBF, Stanford University, CA, to Henry O'Malley, Commissioner of Fisheries, Washington, DC. Located at NARA, Anchorage, AK.

[12] 1) Hungerford, Howard H. 1926. Report of operations at Karluk Weir (Lower) season of 1926. U.S. Dep. Commer. Bur. Fish. Unpubl. report. 4 p.
2) Hungerford, Howard H. 1926. Report of operations at Upper Karluk Weir, season of 1926. U.S. Dep. Commer. Bur.Fish. Unpubl. report. 5 p. Both located at NARA, Anchorage, AK.

[13] Letter (3 December 1926) from Howard H. Hungerford, Warden, Alaska Service, USBF, Seattle, WA, to Dennis Winn, Agent, USBF, Seattle, WA. Located at NARA, Anchorage, AK.

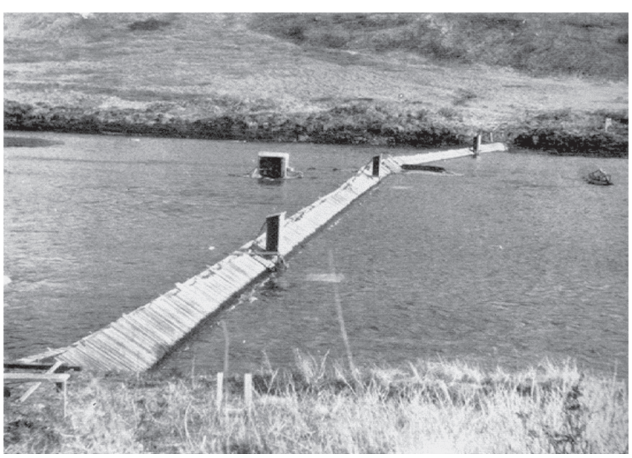
[14] A second weir was temporarily operated at Karluk River Portage in April–June 1927 by the USBF to capture down-migrating steelhead, these being artificially spawned and their eggs incubated in hatchery troughs placed in a nearby creek. This temporary Portage weir for taking steelhead eggs operated each spring during 1927–32 and 1953–59 (Table 3-3).

Table 3-3
List of temporary weirs on the Karluk River, 1927–64.

Year	Agency	Location	Type	Purpose	Operational dates
1927	USBF	Portage	Straight picket weir	Steelhead egg take	April–May
1928	USBF	Portage	Straight picket weir	Steelhead egg take	April–May
1929	USBF	Portage	Straight picket weir	Steelhead egg take	April–May
1930	USBF	Portage	Straight picket weir	Steelhead egg take	April–May
1931	USBF	Portage	Straight picket weir	Steelhead egg take	April–May
1932	USBF	Portage	Straight picket weir	Steelhead egg take	April–May
1941	FWS	Portage	Angled half weir	Dolly Varden capture	May
1953	ADF	Portage	V-shaped picket weir	Steelhead egg take	April–May
1954	ADF	Portage	V-shaped picket weir	Steelhead egg take	29 April–27 May
1955	ADF	Portage	V-shaped picket weir	Steelhead egg take	30 April–24 May
1955	FRI	Lagoon	Tower	Count sockeye salmon	
1955	FRI	Portage	Tower	Count sockeye salmon	
1956	ADF	Portage	V-shaped picket weir	Steelhead egg take	13-30 May
1957	ADFG	Portage	V-shaped picket weir	Steelhead egg take	4-24 May
1958	ADFG	Portage	V-shaped picket weir	Steelhead egg take	20 April–7 May
1959	ADFG	Portage	V-shaped picket weir	Steelhead egg take	28 April–6 May
1963	BCF	Portage	Straight picket weir	Sockeye travel time and river-spawner estimate	1 Aug.–30 Sept.
1964	BCF	Silver Salmon Cr.	Straight picket weir	Count, tag sockeye	August

and length-weight-sex data. The weir was a useful site to capture and sample the salmon.

Besides these primary tasks, fishery biologists conducted several studies at the weir, perhaps the most important being the smolt marking by Rich and Barnaby. They annually marked and released 50,000 sockeye smolts during 1928–36 to determine their ocean survival. Since smolts temporarily accumulated above the weir during their spring down-migration, this was a convenient capture site. Other studies included the abundance of gill-net marked salmon in 1930 and Dolly Varden migrations during 1937–41. Again, the Karluk weir was well-situated for observing, tagging, and recapturing these fish. The weir was also used to trap and destroy Dolly Varden, and this work filled the crew's spare time.



Karluk River salmon counting weir, lower Karluk River, 1930. (From Bower, 1941)

The financial turmoil of the Depression era was a very difficult period for the USBF at Karluk because of limited and uncertain funding for fisheries programs. Commissioner of Fisheries Frank Bell fired many permanent fisheries employees and most temporary workers in 1933, including some at the Karluk weir. He also closed the Afognak hatchery on 30 June 1933. The financial uncertainty continued for several years, and at times the Karluk weir program appeared close to ending, but funds were eventually reinstated. Wage costs at the Karluk weir were $2,486 in 1934 and $2,606 in 1936. Tight funding in 1936 caused Bureau warden Charles Turner to recommend that "if the allotment cannot be increased by at least $2,000, I suggest the weir program be curtailed."[15] Such drastic action never occurred and the Karluk weir program somehow managed to continue operating through these lean financial years.

Although installation and operation of the Karluk River weir followed a similar pattern each year during 1928–41, a few unusual occurrences occurred:

1) High water and ice altered the river channel in the winter of 1929–30. This required the 1930 weir to be moved 15 m downstream from its normal 1921–29 location. Since a straight weir could not be built from bank to bank because of the newly eroded channel, the 1930

[15] Turner, Charles. 1936. Report of operations, Kodiak, Afognak Dist., 1936. U.S. Dep. Commer. Bur. Fish. Unpubl. report. Located at ABL Library Files, Auke Bay, AK.

weir had two sections, one running straight across to a small island and another running at an angle upstream to the opposite bank.

2) For unknown reasons in 1938, weir installation occurred much earlier than normal (early April) as ice left the swollen river.

3) Carl Hubbs, an ichthyologist at the University of Michigan, visited the Karluk River weir on 4 August 1939 while investigating Bureau operations in Alaska.

4) Although weir tending was relatively safe, the Bureau's weir foreman James O'Brien fell from the weir and ruptured his left kidney on 21 August 1939. An APA doctor at Larsen Bay first treated him and he later recovered in Seward, Alaska.

5) In 1941 a weir tender intentionally inflated the pink salmon counts by about 100,000. He had heard about the large pink salmon run of 1940 and altered the 1941 counts to match the previous year. Supposedly, he counted 17,000 pink salmon per day before being replaced (5 August), but only 229 per day were counted after his departure. Few pink salmon carcasses littered the river in 1941, and less than 40 carcasses per day drifted against the weir.[16]

6) To aid their charr studies, DeLacy and Morton installed a temporary weir at the Portage in May 1941 using lumber stored at the site during the 1920s–1930s (Table 3-3). This weir angled upstream from the east bank and extended about half-way across the Karluk River. They designed the weir to concentrate and capture down-migrating Dolly Varden for tagging and measurement, but they were urgently called away to install the salmon counting weir on the lower river.

Pink salmon carcasses continued to be a maintenance problem for weir crews in the even years during 1928–40. Carcasses accumulated against the weir in August–September, greatly increasing the crew's workload. Large pink salmon runs occurred at Karluk in 1922, 1924, 1932, 1934, 1936, 1938, and 1940. When carcasses first arrived in late August or early September, the crew cleaned the weir by pewing each carcass to the downstream side. For example, they tossed 25,000 carcasses over the weir on one day in early September 1932. As the season progressed, however, pewing became difficult because decaying carcasses fell off the pew. Additional temporary workers were often hired to help clean the weir and sometimes day and night shifts were needed:

Dolly Varden temporary angled weir, Karluk River Portage, May 1941. (Allan C. DeLacy, from Catherine J. DeLacy, Seattle, WA)

> [Concerning the Karluk River weir, 1934] Mr. Morris Rafn who was in charge of the weir in 1934 worked so hard and dilligently at all hours of the day and night in a vain endeavor to keep the weir in operation that he seriously impaired his health and has been in a sanitarium ever since returning from duty in Alaska.[17]

Whenever rainfall increased the river flows in August–September, carcasses often arrived at the weir faster than they could be removed and this forced the crew to remove picket sections to flush decaying salmon downstream. Failure to open the weir risked its complete washout and destruction. Of course whenever the weir was open, sockeye proceeded upriver without being counted, impairing escapement accuracy. Thus, pink salmon carcasses continued to be the major oper-

[16] Memo (9 November 1942) from Allan C. DeLacy, Assistant Aquatic Biologist. Located at NARA, Anchorage, AK.

[17] Memo (23 January 1935) from J. T. Barnaby, Scientific Assistant, Seattle, WA, to Commissioner of Fisheries. Located at NARA, Anchorage, AK.

ational problem at the lower weir site and the main argument for moving it to another location.

When Barnaby led the sockeye research program at Karluk during 1930–38, he spent much time at the weir and knew of its problems. He often helped the crew clear carcasses from the weir and estimated escapements whenever they opened the weir. Barnaby realized that carcass removal greatly increased the crew's workload. Consequently, following the salmon carcass problems and hospitalization of one worker in 1934, he recommended moving the weir to the Portage.[18]

After similar problems in 1938, Barnaby and DeLacy repeated the recommendation.[19] They believed that the upstream weir site would solve the carcass problem since most pink salmon spawned in the river below the Portage. Since a steelhead weir had successfully operated at that site each spring during 1927–32, a counting weir also seemed feasible (Table 3-3). Additionally, a cabin for the weir crew already existed and a tractor trail provided good access from Larsen Bay. The lower weir site often had poor access when storms in Shelikof Strait prevented vessels from landing at Karluk Spit. During those times, the only access to the lower river required a long trip, first to Larsen Bay, then a hike across the Portage trail, and finally a 20 km float trip down the Karluk River. Since accurate pink salmon counts could not be made at the Portage, they suggested operating two weirs in even years—the lower weir until 20 August and then the Portage weir from 20 August to season's end. This two-weir idea was never tried.

Weir at Karluk River Portage (1942–44)

Following Barnaby and DeLacy's 1939 recommendation and the weir washout from pink salmon carcasses in 1940, the FWS[20] finally decided in 1941 to locate the 1942 weir at the Portage. Obviously, the recurring carcass problem created inaccuracies in the sockeye salmon counts in even years and needed to be resolved. The Portage site seemed to be a good solution.

During the initial debate in the 1920s over the proper weir location, Bureau employee Lucas warned that large masses of aquatic plants grew in the Karluk River upstream of the Portage. Since these plants died and drifted downstream every autumn, maintenance of the Portage weir would require regular removal of plant debris or risk its plugging and washout:

> [Concerning the Karluk River weir at the Portage] I would not recommend that it be constructed at Larsen's Bay Portage on account of the vegetation that would be coming against it and lack of material nearby. During the latter part of the season, the river for several miles above the portage trail is almost a solid mass of water plants which would be coming down against the weir. This grass is noticeable even at the present site, thirty miles farther down.[21]

The FWS likely knew in 1941 of this potential plant problem but considered it trivial. In a brief attempt to assess the seriousness of the problem, DeLacy checked the river at the Portage in May 1941, but he saw few drifting plants. The brief operation of the steelhead weirs each spring during 1927–32 also provided no data about river conditions in the autumn. Yet, the Portage weir had operated in August and early September 1926, apparently without problems from drifting plants.

Even with Lucas's warning about aquatic plants, plans proceeded for the 1942 Portage weir. Lumber for the new weir was delivered to Larsen Bay in August 1941, transported by boat to the head of the bay, and hauled by tractor to the Portage:

> [Concerning preparations for the 1942 Karluk River Portage weir, 1 August 1941] Al & I helped Geo. Skarbo unload weir lumber from *Eider*. Talked to Ferrandini . . . That was a prize *coup de etat* of Al's to get Ralph to dump off the new Karluk [weir lumber] here at Larsen Bay. That should make history up here. After breakfast we spent AM towing a pot scow alongside dock & loading the 60–4 × 6's, 24–2 × 4's & bundles of 1 × 4's. Then after lunch we hooked on to it with both *Gorb*[*uscha*] & *Tscha*[*wystcha*] [2 dories] in tandem & hauled it to Bens [west end of Larsen Bay]—1 to 2:10—& we made a place to pile it & got dinner & unloaded scow at high tide & then came home 1½ hrs to come back bucking tide & wind.[22]

Thus, the Portage weir was installed and operated from May to October 1942. Since the river channel was narrow at the Portage, the new weir's length measured about 30 m less than at the old site and required only 15 horses to cross the river. Weir operations proceeded

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[18] See footnote 17.

[19] Memo (28 November 1939) from Allan C. DeLacy, Junior Aquatic Biologist, and Joseph T. Barnaby, Associate Aquatic Biologist, Seattle, WA, to Acting Commissioner, USBF, Washington, DC. Located at NARA, Anchorage, AK.

[20] In 1939 the Bureau of Fisheries was moved from the U.S. Department of Commerce to the U.S. Department of Interior and in 1940 it merged with the former Biological Survey to form the U.S. Fish and Wildlife Service (FWS).

[21] Lucas, Fred R. 1924. Report of the red salmon census at Karluk Alaska during the season of 1923. U.S. Dep. Commer. Bur. Fish. Unpubl. report. 4 p. Located at NARA, Anchorage, AK.

[22] Morton, William M. 1941 notebook. Located in personal papers of Robert S. Morton, Portland, OR.

without major problems from May to August 1942, but then aquatic plants began drifting downstream. Charles Petry, FWS fishery management agent, stated in his annual report that the weir was briefly out of commission twice from high water, but the real problem was drifting aquatic plants in September:

> [At the Karluk River weir, 1942] The weir foreman, Mr. Joseph Corkill, reports that the Karluk weir was temporarily out of operation during the first four days of September as the result of a cloud-burst. Overnight the river level rose so rapidly that large masses of aquatic plants, chiefly *Ranunculus*, were uprooted and drifted against the weir, producing a dam across the entire river. A short section of the weir washed out and additional pickets had to be removed in order to liberate the impounded water. By September 4 the river had receded sufficiently to permit the necessary repair work to be done, and normal operation was resumed on that day. Relatively few fish were running at the time of the accident, and an estimate will be made of the number that passed upstream while the weir was open.[23]

The weir again went out of operation the last week of September 1942, with the weir tender exclaiming "99 ton of weeds!"[24]

Richard Shuman operated the Portage weir in 1943 and once more fought the aquatic weed battle. Although it was his first field season at Karluk, by mid July he had searched the upper river for a new weir and research laboratory site, his efforts not being motivated by the 1942 weir problems. Instead, there was renewed research interest in the freshwater life of sockeye salmon, and a weir and laboratory near the lake would benefit future studies. Specifically, Shuman looked for a permanent weir site, envisioning a concrete structure designed to count down-migrating sockeye smolts and up-migrating adults. The area just below the lake's outlet fulfilled his requirements for these facilities:

> [Concerning the upper Karluk River, 18 July 1943] Examined area around outlet of lake with view to weir (permanent) in future. About 50 yards below lake seems to be an excellent spot. Bottom composed of medium and large rubble—with a blue clay conglomerate beneath. Excellent bottom for concrete work. No question of weir not being tight. Banks on both sides composed of glacial deposits of gravel and boulders, and should make quite good buttresses for weir or dam, and are sufficiently high. . . . The only thing against this as a weir site would be the heavy waves which come down the lake with strong south winds. A concrete or rock-crib breakwater might be necessary between the open lake and the weir screens.[25]

Shuman found a good building site for the research laboratory on the west riverbank of the lake's outlet and suggested a road route between Larsen Bay and Karluk Lake. The idea for a two-way weir originated from his previous work at Little Port Walter, Alaska, where a similar structure had been built in 1939. During seven field seasons (1943–49), he pursued the idea of a permanent counting weir on the Karluk River.

Events at the 1943 Portage weir soon reinforced Shuman's desire for a new weir site. The weir functioned well until mid August, but then aquatic plants began drifting downstream and the crew repeatedly cleaned these away for the next two weeks. When river flows increased in early September and greater masses of plants arrived at the weir, the cleaning efforts were completely overwhelmed. Soon, the crew removed the weir pickets and ended the salmon counts:

> [Karluk River weir, 2 September 1943] Weeds! Spent entire day cleaning weeds from weir. River up about 12″ this morning—a greater raise would have swamped us entirely.
>
> [5 September 1943] Busy with weir—counting and cleaning. Weeds coming down constantly. We can keep up, however, but a large raise in water level will swamp us. Weeds all up river rotting and ready to let go.
>
> [9 September 1943] Looks like we are in for it. Not many weeds today, but it has rained all day . . .
>
> [10 September 1943] The "worst" arrived! A light rain here all night, but apparently the storm still on at the lake—and yesterday's rain arrived (via the river) in early morning. River up 18 inches. Quite a few weeds on the weir by morning, and by 9:00 AM—Weeds. They came down in great floating patches, plugging the weir faster than we could get rid of them. By 10:00 AM it became necessary to remove gates and pickets from several sections to let the weeds through—and a spot to roll the already-accumulated weeds through. Balls of weeds weighing up to 400–500 pounds thus rolled through. Yet even so we could nowhere nearly keep pace. By late afternoon it was necessary to remove more pickets (otherwise the whole weir might carry away). In many places the water has undermined the pickets, and two horses have settled out of line.—Also had to remove section of pickets near west bank to protect the

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[23] 1) Petry, Charles. 1942. Annual report of operations in the Kodiak District, 1942. U.S. Dep. Interior, FWS. Unpubl. report. 56 p. Located at ABL Library Files, Auke Bay, AK. 2) USBF. 1938–43. Monthly report of activities, 1938–43. U.S. Fisheries Biological Station, FWS Biological Station, and Section of Alaska Fishery Investigations, Seattle, WA. Unpubl. reports (September 1942). Located at NARA, Anchorage, AK.

[24] FWS 1942–46 notebook. Located at NARA, Anchorage, AK.

[25] Shuman, Richard F. 1943 notebook. Located at NARA, Anchorage, AK.

anchor there (some cutting took place during the day). . . . It is quite apparent that a weir cannot be maintained at this place for a late fall count. Only with a large crew of men (8–12)—and floodlights for night work—would make this at all possible. Even then the battle would be in doubt!!! The weir must be placed above this weed crop, if a fall count is to be attained.[26]

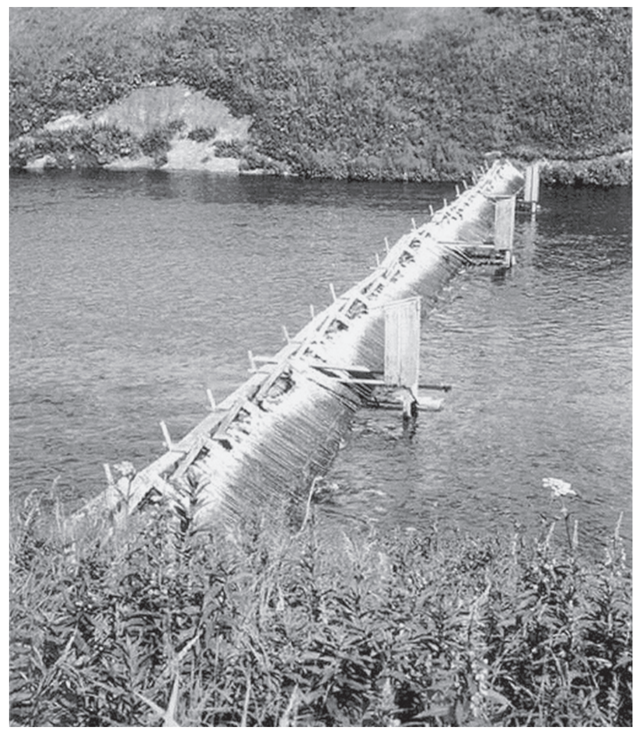
Shuman and his crew continued their heroic efforts for the next week, but huge masses of aquatic plants drifted against the weir. Even with many pickets removed to relieve the water pressure, the structure neared complete destruction. After surveying the river upstream, Shuman finally removed the weir on 20 September, ending the 1943 season several weeks early:

[At Karluk River weir, 18 September 1943] In AM took skiff and outboard and went up river about two miles to look at weed situation. Probably less than 20% have come down. All are rotting and occasionally one gives way. A real bunch of weeds due at next rain. Next wind will bring them, too, for both shores are lined with loose weed, and a wind will blow them loose. Hate to make the move, but can see no hope of replacing weir or keeping it in if we could replace it.[27]

After the problems of 1942–43, the FWS decided to move the weir upriver to Karluk Lake's outlet, though logistically it was impossible to get the lumber and supplies to the new site prior to the 1944 field season. At the time, the Karluk research program lacked the labor-saving benefits of air transportation. Instead, all weir materials had to be hauled across the Portage by tractor and sled, and then boated 14 km upriver to the new site. The FWS Scientific Division purchased a new Cletrac AG caterpillar tractor for the Karluk fisheries program in 1939 and this gave workers reliable transportation across the Portage trail.[28] In 1944 the Karluk field crew (four men) spent most of the summer hauling lumber and supplies from Larsen Bay to Karluk Lake's outlet, reportedly making 25 round trips (36 km each) before completing the arduous task.[29] Moving the materials upriver was particularly grueling, requiring them to physically pull and push heavily loaded boats 14 km against swift currents. Nevertheless, by summer's end the necessary lumber and supplies were ready for the 1945 weir season.

Operations at the 1944 Portage weir proceeded as in 1943, with aquatic plants causing major problems in

FWS Cletrac tractor and sled, Karluk, 1944. (Jerrold M. Olson, Auke Bay, AK)



Karluk River salmon counting weir at the Portage, 1944. (Jerrold M. Olson, Auke Bay, AK)

the autumn. Further, 500,000 pink salmon passed through the weir and most of these spawned and died in the river between the Portage and lake. Pink salmon carcasses added to the aquatic plants floating downstream and forced removal of the weir on 1 September 1944, well before the sockeye runs ended. Thus, after trying to operate a weir at the Portage for three years, the FWS declared it to be a poor site:

[At Karluk River Portage weir, 1944] By late August aquatic plants in quiet section of river above weir began drifting against weir, mixed with thousands of dead spawned-out pinks. From August 27 to August 31

26 See footnote 25.
27 See footnote 25.
28 Shuman made an unsuccessful attempt in May 1944 to drive the Cletrac tractor from the Portage trail to Karluk Lake.
29 The 1944 crew included Richard F. Shuman, Don C. Yates, Jerrold M. Olson, and George D. "Dad" Shuman.

crew was split into day and night crews to keep river detritus from weir. This became impossible and on September 1 the weir was removed. This location obviously unfit for weir site.[30]

Weir near Karluk Lake Outlet (1945–75)

1945–57

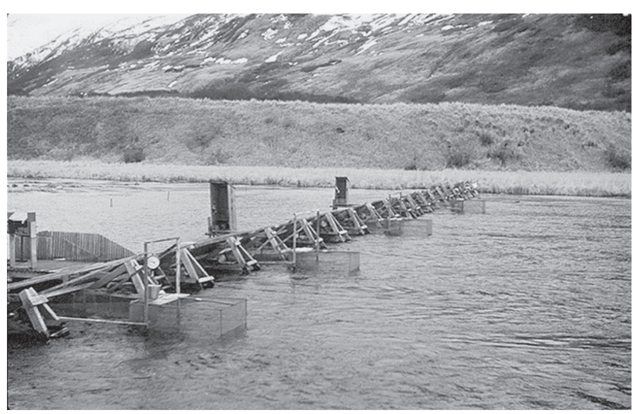
A new wooden picket weir was built on the upper Karluk River in 1945, about 200–300 m below the lake's outlet. After installing the weir, Shuman and his three-man team erected a small weir cabin. The weir operated from mid May to early October without major troubles, confirming Shuman's decision to move the weir. Pink salmon carcasses and aquatic plants were no longer problems. The new location also was advantageous because the FWS research program then, and for the next 25 years, focused on the freshwater life of sockeye salmon at Karluk Lake. Here, the weir crew participated in the studies at the lake, while all the previous crews had been far removed from these activities. This new weir site on the upper river continued without major changes from 1945 to 1957.[31] Though the new location had obvious advantages, three new problems arose: 1) its inaccessibility, 2) matching commercial catches and weir counts, and 3) accounting for sockeye salmon spawning in the upper river below the weir.

In 1945, access to Karluk Lake meant a tedious journey of 18 km from Larsen Bay by tractor, hiking, and small skiff. Supplies only reached the lake with considerable physical effort. To remedy the isolation, in 1945–46 the FWS considered the idea of building a road between Larsen Bay and Karluk Lake, but before this proposal was implemented, access and supply to the lake became relatively simple in 1947 because of frequent flights by several FWS aircraft, especially by Grumman Goose NC–709 and NC–710. Thereafter, the need for an access road was seldom mentioned.

Though aircraft were increasingly common around Kodiak Island in the 1930s and early 1940s, they were not

North end of Karluk Lake and salmon counting weir located in upper river near lake's outlet, May 1957. (Auke Bay Laboratory, Auke Bay, AK)

Karluk River salmon counting weir and cabin near Karluk Lake's outlet, ca. 1952. (Charles E. Walker, Sechelt, BC)



Karluk River salmon counting weir, with four smolt traps built into the weir, 1955. (Clark S. Thompson, Shelton, WA)

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[30] FWS. 1944. Karluk weir, 1944 (Portage Trail Site). Unpubl. report. 1 p. Located at NARA, Anchorage, AK.

[31] Three FWS fishery biologists directed the weir operations during this period: Richard F. Shuman (1945–49), Philip R. Nelson (1950–56), and John B. Owen (1957). In addition to the sockeye counting weir near the lake, a second weir temporarily operated each spring at the Portage during 1953–59. Each year in April-May, a V-shaped weir captured steelhead for artificial spawning, the eggs being shipped to Devil's Creek hatchery on Kodiak Naval Base for incubation. The temporary weir was removed prior to the spring-run sockeye migrations (Table 3-3).

used then by the USBF and FWS to assist fishery biologists because of difficult economic times and World War II restrictions on air travel. After the war ended, the use of nonmilitary aircraft greatly increased around Kodiak Island, and this mode of travel completely changed the old methods of transporting and supplying biologists at Karluk Lake. These aircraft greatly benefited Karluk's biologists by freeing them from the many mundane logistical tasks and expanding their research possibilities. Likewise, biologists stationed at Karluk Lake also benefited from more reliable radios that kept them in contact with other areas of Kodiak Island.

A second problem of the new weir site was the unknown relation between the commercial catches and weir counts of sockeye salmon. Because it took a number of days for adult sockeye to migrate 40 km from the ocean to Karluk Lake, an unknown lag time existed between catch and escapement. Shuman and Nelson partially solved this problem in 1945–46 by measuring the travel times of sockeye, tagging them in the lower river and then recording when they reached the lake weir.

FWS Grumman Goose NC709, Karluk Lake, 1950. (E. P. Haddon, FWS National Digital Library, FWS-1300)

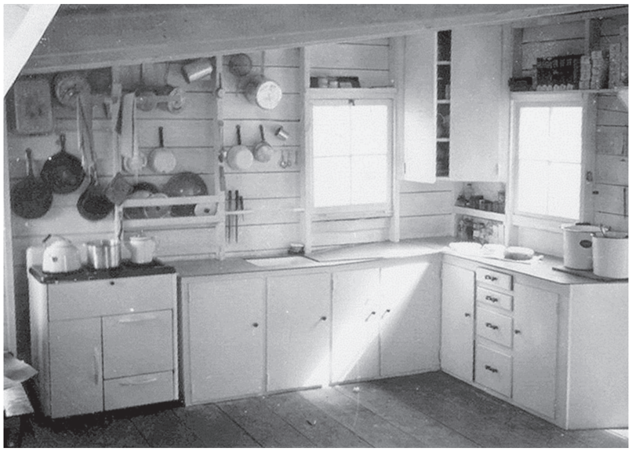
FWS Grumman Goose N709, Karluk Lake, 1954. (Clark S. Thompson, Shelton, WA)

A final problem of the new weir was its location within the river spawning area of fall-run sockeye. Thousands of sockeye spawned in the 200–300 m river reach between the weir and lake and for 2–4 km downstream. Since this weir location failed to count the fish that spawned downstream, it was necessary to estimate that group. Furthermore, some biologists claimed that the weir hindered the free upstream-downstream movements of adult and juvenile sockeye in the upper river (Thompson, 1950; Van Cleve and Bevan, 1973). As adult salmon home to a specific spawning site they often overshoot it, but later return to the exact location. The biologists reasoned that once river-spawning salmon passed through the weir, it formed a barrier to later downstream movement. Likewise, they felt that newly emerged fry that migrated upstream to the lake had difficulty passing through the weir.

Over the next 20 years, all of these hindrance issues were addressed and found to be inconsequential.[32] Direct observations showed that adult sockeye, whether moving upstream or downstream, easily found open weir gates and passed through the weir. In fact, daily weir counts occasionally were negative when more fall-run adults moved downstream than upstream. For sockeye fry, most of the first upstream wave of these young fish had already migrated from the river to the lake before the weir was installed each spring. Typically, later fry migrated upstream along the west river bank, where they easily bypassed the weir through a section of large-meshed wire netting placed to block the adults. For the fry that migrated along the east river bank, the weir was modified with baffles to slow the current and aid their passage.

Pink salmon carcasses rarely were problems at the new weir site, but sockeye carcasses regularly drifted

[32] BCF biologists Richard Gard, Benson Drucker, and Charles DiCostanzo, with more than 15 years of combined experience in operating the Karluk River weir near the lake's outlet, felt that the weir had minimal effects on migrating sockeye salmon adults and fry.
1) Letter (2 June 1972) from Charles J. DiCostanzo, Deputy Laboratory Director, ABL, Auke Bay, AK, to Richard Van Cleve, College of Fisheries, FRI, University of Washington, Seattle. Located in ABL files, Auke Bay, AK.
2) Letter (5 July 1972) from Ben Drucker, Technical Advisory Division, NMFS, Washington, DC, to Reuben Lasker, NMFS. Copy in the personal papers of Richard Gard, Juneau, AK.
3) Letter (10 February 2005) from Richard Gard, Juneau, AK, to Richard L. Bottorff, South Lake Tahoe, CA.



Interior of Karluk River weir cabin, near Karluk Lake's outlet, 1945. (Jerrold M. Olson, Auke Bay, AK)

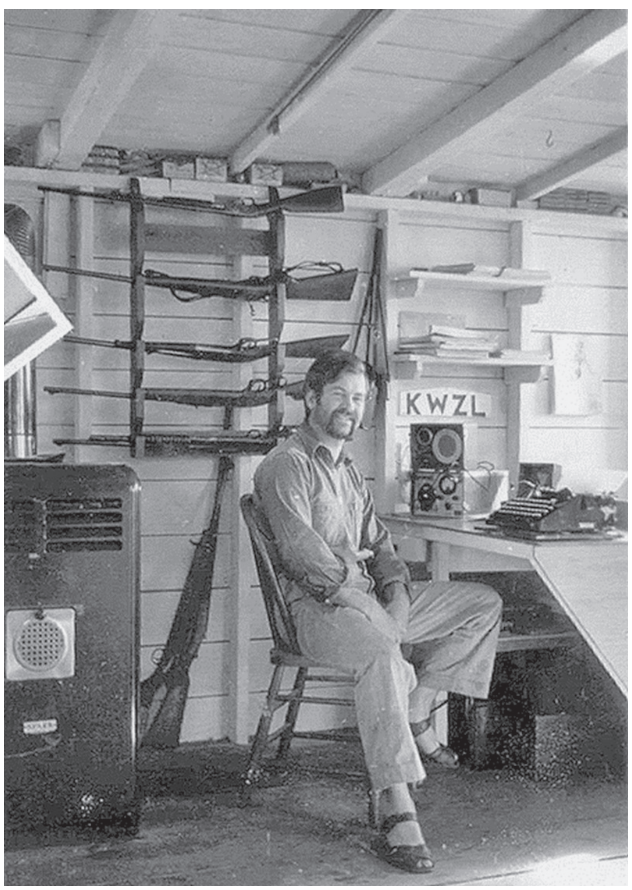
Karluk River weir cabin, pantry, and bunks, 1945. (Jerrold M. Olson, Auke Bay, AK)

against the weir each autumn. These seldom threatened the weir's integrity, but they added to the crew's maintenance chores. For example, in 1945 about 30,000 sockeye spawned in the river above the weir and many carcasses accumulated on the weir face. Similarly in late 1948, several hundred or thousand sockeye and pink salmon carcasses were removed daily. Strong south winds blowing down Karluk Lake occasionally carried debris into the upper river where it collected on the weir and required removal.

Though the counting weir successfully operated near the lake's outlet in 1945, Shuman was not satisfied—he wanted a permanent two-way weir on the upper Karluk River. Accurate measurements of up-migrating adult sockeye and down-migrating smolts were valuable data for the fisheries program. The river just below the lake's outlet suited his plans for a concrete weir.[33] Shuman formally proposed the idea to FWS officials in 1946–47 and estimated the costs at $20,000 for the two-way weir, plus additional expenses for a house and laboratory, a road from Larsen Bay, and auxiliary weirs on several Karluk Lake tributaries.

Response to his idea must have been favorable since engineers surveyed the proposed site in late July 1948, producing detailed topographic maps. To determine the strength of river forces and ice action that would press against a permanent weir, Shuman had wooden posts driven into the river's substrate in November 1948 and left them over the winter.[34] A full set of engineering drawings showing all construction details of the two-way weir, including a fish ladder on the east bank, were completed in May 1949.[35]

Shuman attempted to build the permanent weir on the upper Karluk River during the 1949 field season using FWS resources, his assistant Philip Nelson, five



Jerrold Olson, Karluk River weir cabin, 1945. (Jerrold M. Olson, Auke Bay, AK)

[33] See footnote 25 (18 July).
[34] Freeman, Arthur. 1948 notebook (3 November). Original notebook in personal papers of Arthur Freeman, Indianapolis, IN.
[35] The two-way weir project was known as FWS Construction Job No. 5213.

summer employees,[36] about ten laborers, and support from the U.S. Navy's base at Kodiak. Arriving at Kodiak in May, Shuman arranged with the Navy to use an LCT for transporting lumber and construction supplies to Larsen Bay, a tug for transporting equipment to Larsen Bay, and a TD9 bulldozer for excavating weir foundations. Despite these plans, the Navy bulldozer was useless because it could not be driven to Karluk Lake. On the first attempt, it immediately mired in the soft muskeg after leaving the Portage tractor trail, far from the lake. Extracting the bulldozer and returning it to Larsen Bay required several days.

Undaunted, Shuman decided to drive the lighter FWS Cletrac caterpillar tractor from Larsen Bay to Karluk Lake. This proved to be a difficult two-day ordeal over unstable ground, through thick brush, and across a temporary bridge at Silver Salmon Creek, but the tractor and sled eventually reached Karluk Lake. FWS Grumman Goose 709 and a Norseman airplane hauled 150 tons of lumber, construction materials, and equipment from Larsen Bay to Karluk Lake in mid June. The tractor and sled hauled the supplies from the lakeshore downriver a short distance to the project site, slightly below the 1949 picket weir.

Shuman began excavating the weir foundations in mid June using the tractor and a slip scraper, a combination that worked well, but slowly. He built a small cofferdam to isolate the excavation from the river and installed pumps to remove seepage water. Excavations continued for five days, but the pumps failed to remove inflowing water fast enough and the sides kept slumping back into the hole. Finally in late June, Shuman ended the work:

> [At upper Karluk River just below lake's outlet, 29 June 1949] Dug all AM. Going fairly well until within 24" of bottom. Water impossible to keep out. Jaeger pump very poor—keeps losing prime. Gravel pouring in at sides. Bulkhead will not keep it out. At 4:00 PM gave up. Will go to Kodiak and report complete failure. First job that has completely stopped me.[37]

No further attempts were made to build a permanent two-way weir at Karluk, though Shuman continued until at least 1951 to recommend an accurate measurement of the smolt migration.[38]

[36] FWS summer employees at Karluk in 1949 were Raymond N. Breuser, James Kindler, Charles J. Hunter, John S. Crawford, and George D. Shuman.

[37] Shuman, Richard F. 1949 notebook. Located at NARA, Anchorage, AK.

[38] Shuman, Richard F. 1951. Trends in abundance of Karluk River red salmon with a discussion of ecological factors. Manuscript prepared for *Fishery Bulletin* 71, vol. 52. Unpubl. 56 p. Located at ABL, Auke Bay, AK.

Coffer dam for construction of a two-way permanent salmon counting weir, upper Karluk River, June 1949. (Richard F. Shuman, Auke Bay Laboratory, Auke Bay, AK)

Excavating footing for a two-way weir, upper Karluk River, June 1949. (Richard F. Shuman, Auke Bay Laboratory, Auke Bay, AK)

The wooden picket weir continued to be operated each year during 1945–57 near the lake's outlet, and fairly accurate counts of sockeye salmon were obtained.[39] Nevertheless, the weir had a serious unsolved problem—it was located within the spawning area of fall-run sockeye and possibly obstructed their homing movements. In 1950 William Thompson expressed the belief that "every weir, which hinders the process of trial and error by to and fro or up and down migration, is preventing the homing of individuals to their own best environment, one which may vary widely within

[39] In 1951 new weir lumber was purchased in Seattle, shipped to Zachar Bay on the vessel *Dennis Winn,* and flown to Karluk Lake.

Using a slip scraper and Cletrac tractor to excavate the footing for a two-way weir, upper Karluk River, June 1949. (Richard F. Shuman, Auke Bay Laboratory, Auke Bay, AK)

the same stream." His colleagues at the University of Washington and the Fisheries Research Institute—Donald Bevan, Charles Walker, and Richard Van Cleve—shared similar views

1958–59 Counting Tower

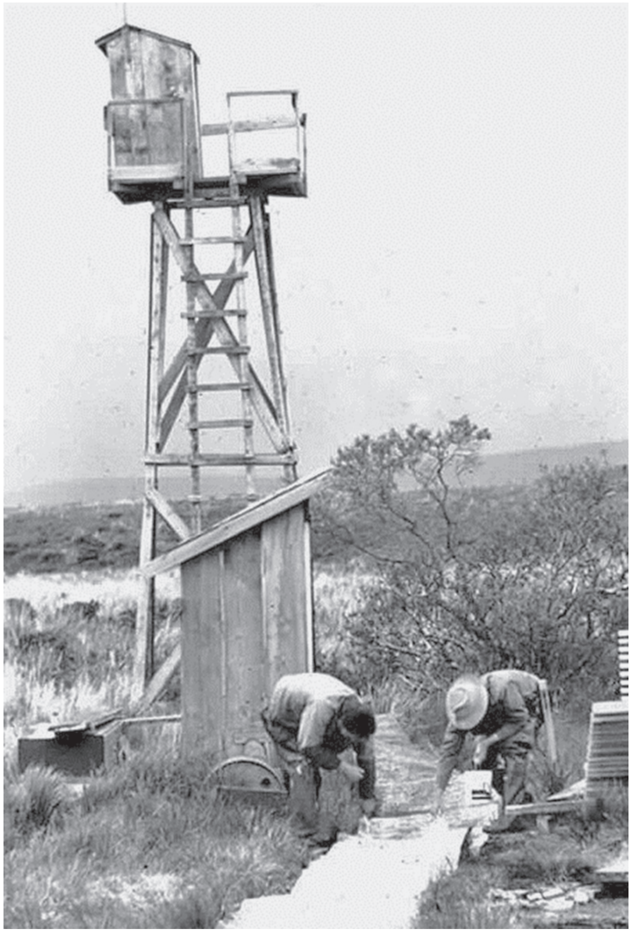
One alternative to a wooden picket weir was a counting tower, an elevated platform positioned on the riverbank with good views across the river. The main advantage of this method was that no physical structure was placed in the river to impede the free movements of adult and juvenile salmon. As salmon migrated past the tower, an observer counted them. In actual practice, rather than constantly manning the tower throughout the day, counting usually occurred for part of each hour and then was proportionally extended for the remaining time. While counting towers appeared to be an elegant simple solution to the problems of picket weirs, in practice, they had some serious drawbacks.

Bevan and Walker, likely at Thompson's direction, explored the Karluk River from lake to lagoon for counting tower sites in 1955. They operated a counting tower at Karluk Lagoon for five weeks, but it proved unsatisfactory.[40] Another site below the Portage was inadequate because surface reflections seriously reduced their visibility.[41] After these preliminary attempts in 1955, Bevan and Walker spent less time at Karluk and devoted no further effort to the counting tower idea. Van Cleve visited the Karluk River weir in 1957 and recommended that it be discontinued, especially during the midseason sockeye salmon run.[42]

Concern that Karluk's wooden picket weir harmed sockeye salmon convinced FWS biologists to try a counting tower in 1958–59. They erected a 6.4 m tower on the east bank of the upper river in 1958, just below the lake's outlet.[43] Observers counted salmon for 10 minutes each hour and then extrapolated the count for the remainder of the hour. Almost immediately, problems arose with the counting tower, the most serious being count accuracy. Counting began at 1:00 A.M. and continued until 11:00 P.M. during the long daylight hours of mid-summer, only stopping for two hours of darkness. At the time, it was unknown if salmon migrated at night; if they did, the counts were inaccurate. As the hours of darkness increased from August to October, this potential counting error increased. To answer the question of night migration, biologists attempted to measure it by using various types and arrangements of artificial lights shining on the river, but this gear often failed or created reflections that made it difficult to see the salmon. Even with adequate lighting, night counts remained inaccurate because distinguishing the different salmon species was often impossible, though Dolly Varden could be distinguished from salmon. Biologists never completely solved the problem of night migration, the best estimate being that it was about 20–30% of day migration.

Further problems existed in identifying salmon from the counting tower. Because the Karluk River was 60–90 m wide at the tower, observers found it difficult to see and count salmon on the far side of the river. To

[40] Bevan, Donald E. ca. 1957. Research activities from 1948 to 1957 inclusive. Kodiak Island Research Fund, FRI, University of Washington, Seattle, WA. Unpubl. report. 2 p. Located in Donald E. Bevan papers, Manuscripts and University Archives Division, University of Washington Libraries, Seattle.
[41] Memo (16 April 1958) from Philip R. Nelson, Fishery Research Biologist, Annapolis, MD, to W. F. Royce, Assistant Regional Director in Charge of Research. Located at NARA, Anchorage, AK.
[42] Owen, John B. 1957 notebook (18 July). Original notebook from the personal papers of John B. Owen, Grand Forks, ND; to be donated to NARA, Anchorage, AK.
[43] BCF. ca. 1958. Fish counts at Karluk Lake. Unpubl. report. 13 p. Located at NARA, Anchorage, AK.

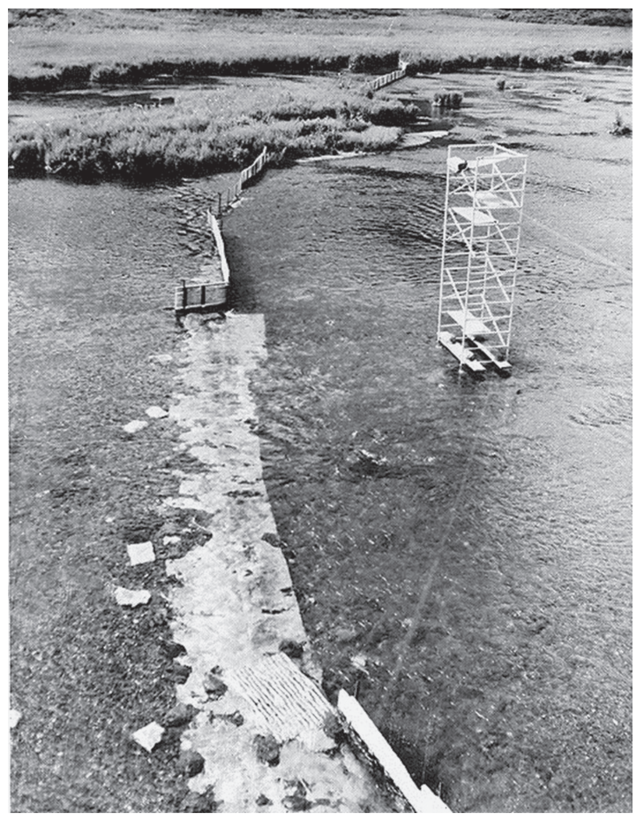


Counting tower used to enumerate adult sockeye salmon, upper Karluk River, June 1958. (Auke Bay Laboratory, Auke Bay, AK)

remedy this, they installed a fence across part of the river, leading the salmon toward a 20 m wide opening nearer the tower. To further improve visibility, they placed white panels (2.1 m wide) on the river bottom to increase contrast between the salmon and substrate. These changes improved the counting effort, but altered the salmon's migratory behavior. First, just as the previous wooden picket weir had done, the installed fence hindered the downstream movements of salmon. Second, the white river panels made salmon reluctant to continue upstream. They gathered just downstream of the panels until a sufficiently large school had accumulated, and then rapidly crossed the white strip in a flowing mass. The white panels needed constant cleaning since passing fish covered them with gravel.

Additional problems occurred when large numbers of sockeyes passed the tower faster than they could be counted. Surface reflections occasionally obscured the salmon, though polarizing sunglasses helped visibility. When river-spawning sockeyes were present each autumn, fish moved both upstream and downstream past the tower and this required that counts be tallied in both directions to determine the net migration. Counting was further complicated in autumn since both unspawned and spawned-out sockeyes moved downstream past the weir; counts of only the former were subtracted from the upstream migration. Therefore, observers had to tally salmon numbers moving in different directions and also instantly recognize species and spawning condition from a long distance—this supposedly simple task was overwhelming.

If the above difficulties were not enough, further problems arose while trying to collect scales and run composition data from sockeye salmon. To do this, biologists built a trap to collect salmon just upstream from the tower, but most fish avoided the trap. When workers tended the trap, salmon altered their normal upstream migrations past the tower. To capture enough salmon, they were forced to use seines in the river, but these were thought to be biased samples. Finally in frustration, the biologists installed a wooden picket weir downstream from the tower in July 1958 to efficiently collect scales and run composition data.



Light tower, guide fences, and white substrate section to help count adult sockeye salmon, upper Karluk River, 1958. (John B. Owen, Auke Bay Laboratory, Auke Bay, AK)

Despite the frustrations and uncertainties of 1958, biologists again used a counting tower at Karluk in 1959. Since the previous tower had blown down during the winter, they erected a new tower in the spring. Operation of the 1959 tower proceeded similarly to that experienced in 1958. Biologists continued experimenting with ways to improve the counts and solve problems, but uncertainties and frustrations remained. Consequently, following the 1959 field season when the FWS reviewed the effectiveness of the 1958–59 counting towers, few positive arguments were given for continuing with this method.[44] Because of the various fences and traps placed in the river, the overall open area for free migration was rather limited, possibly making it more difficult for adult sockeyes to move downstream than with the previous picket weir.

A particularly sharp criticism of the counting tower was the uncertainty it introduced into the sockeye salmon counts, the vital data needed by fisheries managers and researchers. Night migration and species identification problems remained unsolved. Questions also continued about the accuracy of extrapolating 10-minute counts to the whole hour. No evidence existed that the counting tower significantly benefited the sockeye fry that migrated upstream along the riverbanks. Finally, the counting tower required additional labor to operate and this diverted time and effort away from ongoing research programs. Therefore, the FWS abandoned the Karluk River counting tower after the 1959 field season and it was not tried again for many years.

1960–66 BCF–ADFG Transition of Responsibilities

Installation and operation of the Karluk River weir was the sole responsibility of several federal agencies from 1921 to 1959, including the USBF (1921–39), FWS (1940–55), and BCF (1956–59). The State of Alaska assumed full responsibility for managing Alaska's fisheries on 1 January 1960, but because the BCF had an ongoing research program and facilities at Karluk, they continued to support the weir for a number of years. Therefore, the wooden picket weir was installed and operated at Karluk Lake's outlet under the joint responsibilities of the ADFG and BCF during 1960–66, a period of transition when both agencies contributed to its costs and labor. Initially, the BCF installed and maintained the weir since the data collected were vital to their sockeye research, and this effort continued through 1969. The ADFG assigned one person to help at the weir during 1960–63; they contracted weir installation and operation to the BCF and provided funding for 1964–66.

The rationale for the Karluk River weir and its operations slowly changed after 1960, though this did not become obvious until the 1970s. When ADFG assumed their management responsibilities in 1960, these included the state's commercial, sport, and subsistence fisheries. Though the primary purpose of the Karluk River weir was to collect data on the commercially important sockeye salmon, over the years much biological information had been obtained about other salmonid fishes. Biologists studying these other fish species recognized the weir's value and suggested modifications to aid their research. Richard Marriott, ADFG sport fish biologist, suggested in 1967 that a counting tower or weir be operated on the lower Karluk River to gather data on fall-run coho salmon and steelhead. Implementation of his idea was years away, but it showed the growing interest in using the weir for other purposes than to count sockeyes. Significantly, Marriott's recommendation called attention to the impracticality of the existing weir site at the lake's outlet when studying Karluk's other fish species.

In addition to the main Karluk River weir, several secondary weirs briefly operated on the upper river for specific studies in the 1960s. Gard (1973) operated a second weir at the Portage from early August to late September 1963 (Table 3-3). He tagged adult sockeyes at the Portage and measured their travel time over the 14 km to the main weir. Further, using mark-and-recapture techniques, he estimated that the number of fall-run sockeyes that spawned in the Karluk River below the main weir was 10% of the total escapement (Gard and Drucker, 1965). This correction was then applied to subsequent weir counts. Another temporary weir was operated on the Karluk River near Silver Salmon Creek in late 1964, about 5 km downstream from Karluk Lake, again to estimate fall-run river spawners.

Although not directly related to the Karluk River weir, in 1964 while investigating the Terror Lake hydroelectric project on northeast Kodiak Island, the U.S. Bureau of Reclamation briefly evaluated a similar plan for Karluk. The Larsen Bay hydroelectric project included plans for a dam near the Karluk River portage that raised Karluk Lake by 4.6 m and a penstock (3 m diameter) feeding a 30,000 KW power plant on Larsen

[44] BCF. ca. 1959. Justification for replacement of Karluk Tower operation with weir. Unpubl. report. 6 p. Located at NARA, Anchorage, AK.

Bay. Apparently, once the significant impacts on Karluk's fish and wildlife were emphasized by BCF Regional Director Harry L. Rietze and ADFG Commissioner Walter Kirkness, no further efforts were made to pursue this project.[45]

1967–75 ADFG Weir Operation near Karluk Lake Outlet

The ADFG assumed full responsibility for operating the Karluk River weir in 1967, partly because of changing federal and state budgets. Since BCF funding was then limited, it was difficult for them to continue with both the sockeye research and weir operations at Karluk. In contrast, ADFG then received additional funding for fisheries programs after passage of the federal Anadromous Fish Act in 1967. Consequently, following the 1966 field season, the BCF requested that ADFG take over weir operations, collection of run-composition data of adult sockeye, and enumeration of sockeye smolts:

> [Concerning the Karluk River weir, 1967] Due to budgetary limitations and the resignation of Richard Gard from the Karluk Lake project, it is requested that the Alaska Department of Fish and Game assume responsibilities for the Karluk River weir, sampling of the adult red salmon escapement, estimate of smolt migration and sampling of red salmon smolts. With the loss of the project supervisor and without foreseeable replacement due to current BCF limitations, the State could more efficiently take over the above mentioned activities.
>
> With funds now available to the State, and with cuts in BCF funding at the present project level resulting in limitation to research, it is certainly more feasible to the mutual benefit of both the Bureau of Commercial Fisheries and the Alaska Department of Fish and Game to have the latter organization take over adult counting and smolt enumeration at Karluk Lake. Since Statehood, counting of the red salmon escapement into the Bristol Bay area has been taken over by the Alaska Department of Fish and Game. In the last several years, they have assumed the duty of smolt enumeration in the Kvichak, Naknek and other systems in the Bristol Bay area. Under the new Anadromous Fish Act, enumeration of adults and smolts at Karluk Lake by the State would be a natural extension of their province.[46]

In actual practice, the BCF installed the Karluk River weir during 1967–69, analyzed the sockeye salmon scales, and conducted the smolt studies, while the ADFG operated the weir and collected the run composition data on adult sockeyes. These mutual operations continued until the BCF ended its research program on Karluk's sockeye in 1969.

The ADFG continued to operate the Karluk River weir near the lake's outlet during 1967–75. They improved the weir in 1972–73 by replacing the wooden pickets with 2.5 cm aluminum pipes. These smooth pipes allowed sockeye smolts to easily pass through the weir and decreased maintenance since less debris caught on the weir. Even so, the ADFG encountered some problems during those nine years. In 1967, 1968, and 1972 unspawned, fall-run sockeyes unexpectedly died (perhaps from warm lake temperatures) and drifted against the weir (Blackett et al., 1969).[47] Heavy rains in late May and early June 1969 washed out the weir until 11 July. The same year a crew member shot a brown bear trying to enter the weir cabin.[48] In 1972 picket sections were removed for two days to let 20,000 adult sockeyes move downstream to spawn in the river below the weir.[49]

The ADFG decided in 1972 that the existing weir site at Karluk Lake's outlet was unsuitable because of the uncounted sockeyes that spawned in the upper river each fall. Total sockeye escapement was a combination of the fish counted through the weir and an estimate of the river spawners below the weir (about 10% of total escapement). Beyond these counting inaccuracies, the ADFG thought that the existing weir might hinder the homing behavior of river spawners. This view was also held by Van Cleve and Bevan (1973), who believed that the upper river was the most important

[45] 1) Letter (22 April 1964) from U.S. Bureau of Reclamation, Alaska District Headquarters, Juneau, AK, to Harry L. Rietze, Regional Director, USFWS, BCF, Juneau, AK. Located at NARA, Anchorage, AK.
2) Letter (16 April 1965) from Harry L. Rietze, Regional Director, USFWS, Juneau, AK, to George N. Pierce, District Manager, U.S. Bureau of Reclamation, Alaska District Headquarters, Juneau, AK. Located at NARA, Anchorage, AK.
3) Letter (25 May 1965) from Walter Kirkness, Commissioner, ADFG, to Harry Rietze, Regional Director, USFWS, BCF, Juneau, AK. Located at ASA, Juneau, AK.

[46] Memo (20 October 1966) from Benson Drucker, Acting Project Leader, Karluk Lake, Red Salmon Investigations, BCF, Auke Bay, AK, to Laboratory Director, BCF, Auke Bay, AK. Located at NARA, Anchorage, AK.

[47] Lechner, Jack, Martin F. Eaton, Kenneth R. Manthey, Louis A. Gwartney, and Lawrence M. Malloy. 1972. Kodiak area management annual report, 1972. ADFG. Unpubl. report. Located at ASA, Juneau, AK.

[48] Simon, Robert J., Jack Lechner, Martin F. Eaton, and Peter B. Jackson. 1969. Kodiak area management annual report, 1969. ADFG. Unpubl. report. Located at ASA, Juneau, AK.

[49] See footnote 47.

sockeye spawning area in the Karluk ecosystem and that placing a weir within this area harmed its adults and juveniles by impeding natural movements. Their conclusions were based on many years of field observations at Karluk during the 1940s and 1950s by Bevan and Walker. Thus, to improve the counting accuracy and to benefit sockeye movements, the ADFG recommended moving the weir to the lower Karluk River:

> [Concerning the Karluk River weir near lake's outlet, 1972] The present Karluk weir location at the lake outlet is not giving the Department a realistic count on red salmon. We know from lagoon tagging experiments that many of the August fish entering the lagoon spawn in the river and do not pass through the weir. We are proposing that the weir be moved to the Karluk Lagoon where more accurate counts can be made.[50]

Though commercial fisheries biologists at ADFG suggested this weir change in 1972, sport fish biologists also preferred the lower river site to aid their studies. For example, in 1972–73 Van Hulle and Murray (1973) wanted a weir on the lower Karluk River to monitor Chinook salmon populations, but they failed to secure a lease for a new site (Murray and Van Hulle, 1974).

The ADFG operated two counting devices on the Karluk River in 1975, the standard picket weir near the lake's outlet and a counting tower on the lower river near the lagoon. At the lagoon tower, inaccurate sockeye counts made this an unsuccessful one-year experiment; the problems they encountered were similar to those of the 1958–59 BCF towers:

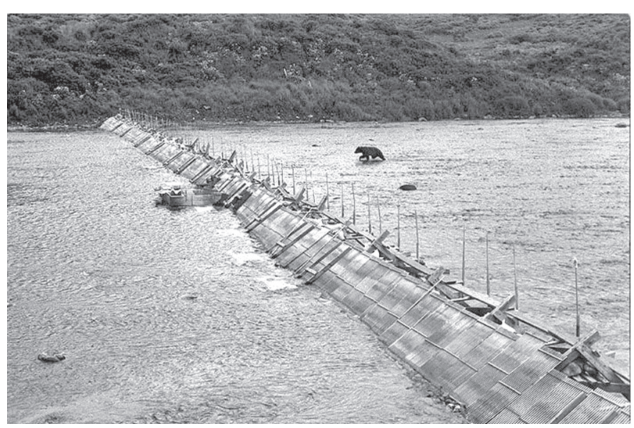
> [At the counting tower on the lower Karluk River, 1975] A cabin, partial weir, flash boards, and counting tower were constructed during the season at Karluk Lagoon. The data obtained from the tower counts proved to be unreliable primarily because of two problems. Salmon passed over the panels during periods of poor visibility and inability to differentiate species of salmon.[51]

Nevertheless, the 1975 counting tower trial was a preliminary step in moving the weir to the lower river. The decision had already been reached that the existing site on the upper river was unsuitable and that a new location on the lower river best satisfied the different interests of the ADFG biologists. Thus, after 30 years of being located near Karluk Lake's outlet, the weir was moved to the lower river in 1976.

Weir near Karluk Lagoon (1976–2010)

The ADFG negotiated a lease with Karluk Village in 1975 to allow a picket weir on the lower river, just upstream from Karluk Lagoon. From 1976 to the present time, the ADFG annually operated the counting weir at nearly the same site on the lower river as that used by the USBF during 1921–41. As expected, the main problem at this location during 1976–2010 was the same as during 1921–41—i.e., even-year pink salmon carcasses drifting against the weir. Weir crews during 1976–2010 once again struggled to clear away pink salmon carcasses in August and September and occasionally removed picket sections to pass the debris downstream (Table 3-1). The ADFG's 1975 experiment with a counting tower was perhaps intended to solve this biennial problem. High river flows irregularly threatened the weir or scoured holes that let salmon pass by uncounted. In some years, bears repeatedly damaged the weir, creating holes that needed timely maintenance to assure an accurate count of the escapement (Spalinger, 2006). In recent years, the ADFG has developed a detailed weir operations manual (Caldentey, 2007, 2009b).

The main purposes of the Karluk River weir during 1976–2010 were to count sockeye salmon and collect run-composition data, but the new location also provided much better information on the other salmonid fishes then being studied (Table 3-2). In particular, it allowed biologists to gather escapement and run composition data on Karluk's Chinook salmon, vital information needed to calculate spawner-recruit relation-



Karluk River salmon counting weir near Karluk Lagoon, 1996. (Richard Lee Bottorff, South Lake Tahoe, CA)

[50] See footnote 47.

[51] Manthey, Ken, Larry Malloy, and Melayna McGuire. 1975. 1975 annual management report, Kodiak Management Area. ADFG, Division of Commercial Fisheries, Kodiak. Unpubl. report. 160 p. Located at ADFG Library, Douglas, AK.

Collecting sockeye salmon scales, Karluk River weir, 1996. (Richard Lee Bottorff, South Lake Tahoe, CA)

ships and to set accurate escapement goals (Nelson et al., 2005). New concerns arose, however, about the effect of the new weir on steelhead survival and movements. Van Hulle and Murray (1977) suggested that the weir may harm spawned-out steelhead by delaying their May–July emigration to the ocean. These downmigrating kelts were in poor condition and delays of a few days or weeks at the weir may reduce their survival. A well-defined method to quickly pass steelhead kelts below the weir was lacking during 1976–91. Begich (1995) concluded that "timely, efficient passage of postspawn downstream migrants in steelhead systems weired for enumeration of immigrating salmon is of paramount importance and greatly assists in facilitation of steelhead emigration." Prior to 1992 the weir delayed steelhead emigration about two weeks, but starting in 1992 a trap was built into the weir to swiftly move kelts downstream. Recent abundant populations of Karluk River steelhead may be partially due to these weir modifications.

The ADFG typically removed the Karluk River weir in mid or late September, well before the entire steelhead and coho salmon runs had entered the river. Van Hulle and Murray (1978, 1979) recommended that the weir be operated until 15 November to get better counts of these two fish species, but this was never done because of logistical problems and deteriorating weather conditions as winter approached. In the 1920s and 1930s, the USBF tried operating the Karluk weir into late October, but abandoned this effort when the weather-related problems became known. Problems with maintaining the weir greatly increased from ice conditions and rising river flows after mid October, often making it hard to remove the weir for winter storage. Weir crews staying into late October often found it difficult to depart because Karluk Lagoon was ice covered, and storms in Shelikof Strait kept USBF boats from landing at Karluk Spit.

Conclusions

This history of the Karluk River weir documents that each of the three weir sites—lower river, Portage, and lake outlet—has certain advantages and disadvantages, some of which have changed with time as different research topics were pursued and logistical problems were solved. Knowledge of these weir sites has been gained by many years of trial-and-error and hard work, by the field efforts of hundreds of biologists and weir tenders, by experiencing a full range of environmental conditions, by field observations of the remarkably dynamic fish migrations, and by discussions between biologists and officials with different research and management interests. After more than 90 years of continuous operation by federal and state agencies, a consensus exists that the lower river is the best weir site, although pink salmon carcasses during even-numbered years may be a problem. This weir site fulfills its main operational purpose of accurately measuring sockeye salmon escapement, but it also provides useful information on many of Karluk's other salmonid fishes. It satisfies the combined concerns and requirements of fisheries management, research, and conservation (Table 3-2).

Despite its times of controversy and various locations since 1921, the Karluk River weir has supplied a tremendous stockpile of fishery and scientific data on its commercial and sport fishes (Figure 1-3). The knowledge gained from this facility, as well as the long-term research at Karluk, has advanced the understanding of sockeye salmon from near complete ignorance in the 1880s to an exquisite appreciation of this complex and dynamic species in 2010. Clearly, the weir continues to be one of the best tools for managing, monitoring, and studying salmonid fish runs in the Karluk River. While the uses of the weir may change somewhat in the future and the operations will be modified and improved, the valuable data gathered each year make it likely this program will continue for many years.

CHAPTER 4

Sockeye Salmon Life History

In diversity lies the salvation of the species.

Karluk River sockeye salmon and the system they inhabit are unique and complex. With the exception of the much larger Fraser River system, the physical geography of the Karluk River complex is probably as varied as any other sockeye salmon river system in North America.[1] The fish spawn in at least five habitat types ranging from the brackish waters of Karluk Lagoon to the torrential cascades of the lateral streams. They spawn over a long period of time from June to November. There are at least 24 different age groups (combinations of freshwater and saltwater residencies)—more than those identified for any other river system. Some Karluk River sockeye salmon smolts migrate to sea the same summer they emerge from the gravel, while others remain in freshwater for up to five years, at which time they are among the largest smolts reported from Alaska lakes. This unique array of diverse traits selected by a varied physical environment has permitted the Karluk River sockeye salmon to survive a changing total environment. Further, this combination of biological and environmental variability has resulted in the highest density of adult sockeye salmon known.

Sockeye salmon are anadromous, which means they spend part of their early lives in freshwater before migrating to the sea, where they remain for a period before returning to freshwater to spawn. Therefore, some system of age designation is necessary to show what portion of an individual's life is spent in each habitat. The earliest investigators to age Karluk River sockeye salmon and to develop a system that conveys this information were Charles H. Gilbert and Willis H. Rich (1927). In their system, total age is given with the number of years spent in freshwater indicated as a subscript. To obtain the number of years spent in the sea, the subscript is subtracted from the total age. The most common type found in the Karluk River is designated as a 5_3. We will briefly follow this age group through its life cycle.

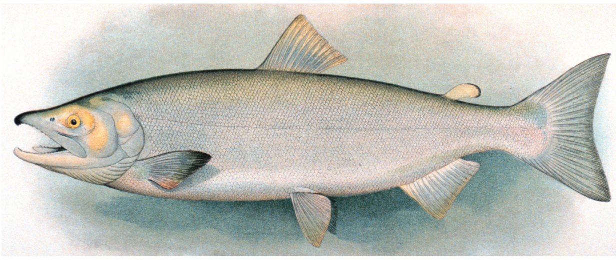
Adult 5_3's return to the mouth of the Karluk River at 5 years of age, swim up the river to Karluk Lake and locate the site of their birth, where they spawn in nests made in the gravel (called redds) and die. The fertilized eggs hatch in the gravel and are now called alevins. In the early spring, the alevins emerge from the gravel after about 10 months. They actively migrate into Karluk Lake as fry, where they feed and grow for a little over two years. Therefore, they remain approximately three years in freshwater from the time when they were deposited as eggs in the redds. In May or June, as smolts they migrate down the Karluk River to the sea. After two years in the ocean this new generation of adults returns to the mouth of the Karluk River, thus completing the cycle. Many variations of this general account occur and are presented in detail in this chapter on life history.

One advantage of the Gilbert and Rich system of age designation is that one can see at a glance the brood year of an individual and predict when the majority of its offspring are likely to return, provided the date of capture is known. Sockeye salmon are often cyclic, and the Gilbert and Rich system is useful in studying this phenomenon. We use the Gilbert and Rich method of expressing sockeye salmon ages in this fisheries research history.

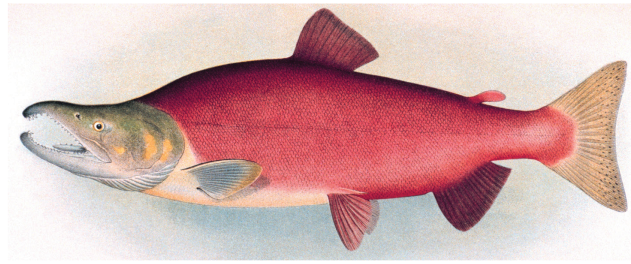
Age Composition of Adults

Age composition of adult Karluk River sockeye salmon was first determined in 1916 by Gilbert and Rich (1927), when scale samples from 382 fish were collected from the seine fishery near Karluk Spit. Subsequently, in 1917, 1919, and 1921, limited numbers of fish from the same source were aged. In 1922, scales from 2,469 fish were aged, but no scales were collected in 1923. Large samples of sockeye salmon scales were generally collected and

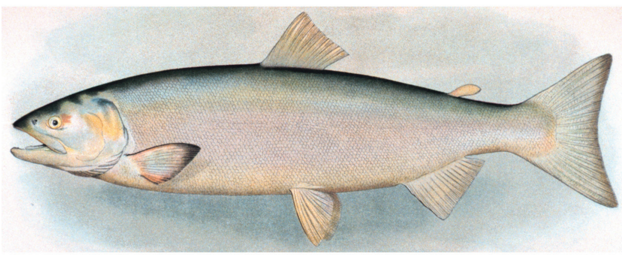
[1] A description of the physical aspects of the Karluk River system is presented in Chapter 1.



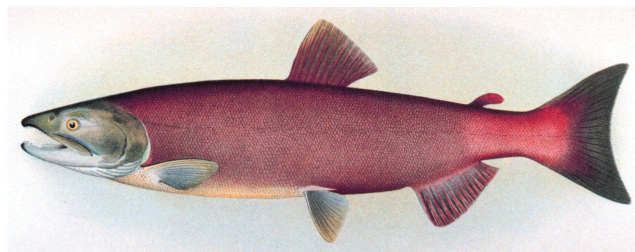
Male sockeye salmon, ocean colors



Male sockeye salmon, spawning colors



Female sockeye salmon, ocean colors



Female sockeye salmon, spawning colors

Ocean and spawning colors of adult sockeye salmon. (Drawings by Albertus H. Baldwin, from Evermann and Goldsborough, 1907.)

aged each year from 1924 to present times (Table 4-1).[2] Length, sex, and, occasionally, weight and fecundity data were also obtained during the sampling process. Between 1964 and 1968, otoliths were collected during the fall sockeye salmon runs because the margins of many late-run scales were badly eroded. These damaged scales resulted in under-assignment of ocean ages. Otoliths were not so affected and would be the preferred structure to use in aging sockeye salmon, except that aging with otoliths is more expensive than aging with scales, and the fish must be killed to obtain the otoliths. It would be a boon to sockeye salmon research if a method were developed that could accurately determine the ocean age without having to kill the fish.

Total age of adults ranged from 2 to 9 years, with 1–5 of those years spent in freshwater as eggs and juveniles and 0–5 years spent in the ocean. Hence, many different age combinations of fresh- and salt-water residencies were possible. A total of 24 different ages have been identified (Table 4-1 and Appendix), including 2_1, 3_1, 3_2, 3_3, 4_1, 4_2, 4_3, 4_4, 5_1, 5_2, 5_3, 5_4, 5_5, 6_2, 6_3, 6_4, 6_5, 7_3, 7_4, 7_5, 8_3, 8_4, 8_5, and 9_5 (Gilbert and Rich, 1927; Barnaby, 1944; Rounsefell, 1958; Barrett and Nelson, 1995). Four of the combinations (3_3, 5_5, 8_3, and 9_5) were reported during one year only with the 9_5 being discovered in 1991 (Barrett and Nelson, 1995) and the 8_3 being first reported in 2009. The 2_1's were reported only three times (1987, 1989, and 2002).

Aging sockeye salmon by reading their scales is as much an art as it is a science. Experienced scale readers sometimes assign different ages to the same fish (Godfrey et al., 1968; Bilton et al., 1983). Hence, one or more of the rare age combinations listed above might not exist in nature, but only in the minds of the scale readers. On the other hand, there may be other valid age combinations that were not present in the samples or identified by the scale readers. Nevertheless, the Karluk River sockeye salmon, with 24 recognized age combinations, exhibit more age variability than any other sockeye salmon system known to us.

The most common age groups of Karluk River sockeye salmon are 5_3, 6_4, and 6_3, listed in descending order of

[2] Table 4-1 is a compilation of data from many investigations. Sampling and analysis methods often differed or were not reported. Some re-calculations were necessary so that all data in this table adhere to the percentage of occurrence format. There may be errors. Therefore, we present this table not as a definitive work, but as a working guide to what we found during our research. If further analysis is desired, we recommend that the original data be located.

Table 4-1
Percentage occurrence of age groups of Karluk River sockeye salmon runs, 1916–2010.[1]

	Age groups																									
	2_1	3_1	3_2	3_3	4_1	4_2	4_3	4_4	5_1	5_2	5_3	5_4	5_5	6_2	6_3	6_4	6_5	7_3	7_4	7_5	8_3	8_4	8_5	9_5	Sample		Data source
	0.1	0.2	1.1	2.0	0.3	1.2	2.1	3.0	0.4	1.3	2.2	3.1	4.0	1.4	2.3	3.2	4.1	2.4	3.3	4.2	2.5	3.4	4.3	4.4	size	Remarks	(taken or adapted from)
1916						0.3	0.5				85.1	1.0			2.9	10.2									382	Fall run	Gilbert and Rich, 1927
1917		0.3	0.1		0.4	0.3				0.9	82.4	0.3			5.3	9.5			0.1						758	[2]	Gilbert and Rich, 1927
1918																											
1919						1.0	1.9			1.9	81.6				7.8	5.8									103	Fall run	Gilbert and Rich, 1927
1920																											
1921										0.9	88.2				5.2	5.2			0.5						211	Fall run[3]	Gilbert and Rich, 1927
1922					0.2	0.8	1.1	0.3		0.6	59.3	1.3	0.1		32.2	4.0	tr		0.1						2469	Total run[3]	Barnaby, 1944
1923																											
1924				tr		0.4	3.2	0.4		0.4	76.0	3.2			5.4	10.5			0.5						5132	Total run[3]	Barnaby, 1944
1925		0.2			tr	0.9	5.2			0.2	66.8	2.3			8.3	15.8	tr		0.3						5513	Total run[3]	Barnaby, 1944
1926		0.1			0.3	2.6	0.5	tr		0.9	81.1	0.2			6.0	7.6	tr		0.6	0.1		tr			8172	Total run[3]	Barnaby, 1944
1927		tr			tr	0.1	2.1	tr		7.9	70.8	2.7			9.6	6.1	tr		0.5	0.2			tr		4963	Total run[3]	Barnaby, 1944
1928					tr	0.4	0.2			tr	56.9	0.4			32.8	9.0			0.3	tr					4247	Total run[3]	Barnaby, 1944
1929					tr	1.0	0.2			0.8	34.8	0.3			26.0	35.1		0.5	tr	1.3					1602	Total run[3]	Barnaby, 1944
1930						tr	4.0			0.6	51.5	11.9			14.5	16.0		tr	1.5	tr					3617	Total run[3]	Barnaby, 1944
1931		tr			tr	0.9	0.5			0.3	49.8	3.0			6.4	38.1	0.1	tr	0.9	tr					7258	Total run[3]	Barnaby, 1944
1932					tr	1.0	0.9			0.8	48.2	2.1			4.5	38.6			3.2	0.7					4700	Total run[3]	Barnaby, 1944
1933					tr	0.5	0.4			2.0	52.3	1.3			13.1	27.9	tr	tr	1.3	1.2					3867	Total run[3]	Barnaby, 1944
1934						0.7	0.2			1.7	32.0	1.0			35.7	25.7	tr		2.9	0.1			tr		6551	Total run[3]	Barnaby, 1944
1935			tr		0.1	2.7	4.2			2.0	24.1	5.4		0.2	19.7	32.8	0.5	0.1	6.2	1.9		tr	0.1		7152	Total run[3]	Barnaby, 1944
1936		tr			tr	0.5	1.3	tr		2.2	69.9	3.2		tr	6.2	13.1	tr	0.1	2.5	1.0		tr	tr		7093	Total run[3]	Barnaby, 1944
1937			tr			0.6	2.2			1.0	68.0	1.8			7.6	16.6	0.2	tr	0.8	0.1			1.0			Total run[3]	Rounsefell, 1958
1938						2.6	0.6			1.5	59.9	0.2			16.4	16.7	tr	tr	1.0	1.1			tr			Total run[3]	Rounsefell, 1958
1939			tr			0.1	0.7			1.7	29.4	3.2			45.1	12.3	0.2	0.1	6.6	0.4		0.1	tr			Total run[3]	Rounsefell, 1958
1940					tr	0.6	0.6		x	0.2	33.0	5.1		tr	23.8	32.0	0.1	0.3	3.9	0.3		tr	tr			Total run[3]	Rounsefell, 1958
1941						0.4	0.8			0.4	51.2	2.4		x	11.8	29.1		0.2	3.5	0.2		tr	tr			Total run[3]	Rounsefell, 1958
1942					0.1	0.8	2.2			0.9	52.9	0.9			10.2	24.2		0.1	7.6				0.1			Total run[3]	Rounsefell, 1958
1943					0.5	0.6	0.9			2.0	55.0				23.0	14.2			3.6	0.1		0.1				Total run[3]	Rounsefell, 1958
1944		0.1	tr		0.1	0.8	0.3			3.5	56.5	1.0		tr	25.5	8.9		0.2	3.1	0.1		0.1	tr			Total run[3]	Rounsefell, 1958
1945			tr			0.9	0.2			9.5	19.8	0.1		tr	49.9	13.4		0.3	5.8	0.1		0.2	tr			Total run	Rounsefell, 1958
1946			0.1		tr	0.8	0.2			3.4	18.3	1.1		0.1	31.7	30.5		1.0	12.3	0.3		0.1	tr			Total run	Rounsefell, 1958
1947			tr			0.8	2.9			2.1	26.6	4.9			26.2	30.7		0.1	5.4			0.2				Total run	Rounsefell, 1958
1948						0.1	0.5			0.5	71.1	0.1			8.9	14.2		0.2	4.3	0.1						Total run	Rounsefell, 1958
1949						0.1	0.3			0.1	52.3	0.1			20.2	20.2	tr	0.1	6.0	0.3		0.1	tr			Total run	Rounsefell, 1958
1950							0.1				29.1	0.4			47.1	11.2		0.1	11.8	0.1			tr		2705	Total run	[4]
1951							2.0			0.2	23.8	0.6		0.1	15.9	54.8	0.1	0.2	0.8	1.7					1910	Total run	[4]
1952						0.3	1.8			0.5	52.3	3.1			5.2	12.0			22.1	x						Total run	[5]
1953					tr	0.4	0.8			0.1	52.3	0.5			9.8	28.4			6.3	x			x			Total run	[5]
1954						0.6	0.4			0.7	47.0	2.1			12.9	34.7			2.1	x			x			Total run	[5]
1955						0.1	1.1				17.3	2.2			15.1	58.7			5.4	0.1						Total run	[5]

Table 4-1 (cont.)

Percentage occurrence of age groups of Karluk River sockeye salmon runs, 1916–2010.[1]

	Age groups																									
	2_1	3_1	3_2	3_3	4_1	4_2	4_3	4_4	5_1	5_2	5_3	5_4	5_5	6_2	6_3	6_4	6_5	7_3	7_4	7_5	8_3	8_4	8_5	9_5	Sample		Data source
	0.1	0.2	1.1	2.0	0.3	1.2	2.1	3.0	0.4	1.3	2.2	3.1	4.0	1.4	2.3	3.2	4.1	2.4	3.3	4.2	2.5	3.4	4.3	4.4	size	Remarks	(taken or adapted from)
1956						x	4.6			tr	49.1	3.4			21.2	19.9	x		1.7	x			x		3236	Total run[6]	[7]
1957			tr			0.1	5.1			0.1	52.4	3.3			13.3	24.0			1.7						3670	Total run[6]	[7]
1958						0.2	4.2				42.6	9.1		0.1	5.4	36.0	0.1		2.1	0.2					2080	Total run[6]	[7]
1959							1.5			0.1	51.5	3.5			10.0	28.9			4.6	0.1					3185	Total run[6]	[7]
1960			tr			tr	1.5			tr	44.4	0.7			13.9	37.3			2.2						>3914	Total run[6]	[7]
1961			0.1			1.2	7.6			1.4	44.4	1.8			16.2	23.1		0.1	4.1	0.1					1760	Total run[6]	[7]
1962			0.1			0.1	2.6			1.1	78.3	0.5		0.1	9.9	6.2			1.2						2237	Total run[6]	Gard and Drucker, 1963
1963						0.7	0.5			0.1	41.2	1.7			20.5	19.2			16.1						2022	Total run[6]	Gard and Drucker, 1965
1964						0.4	0.8			0.2	50.8	4.1			9.5	32.1		tr	1.2	0.9					2410	Total run[6]	Gard and Drucker, 1966a
1965										0.4	26.0	2.6			8.3	59.4		0.1	3.3						1712	Total run[6]	Gard and Drucker, 1966b
1966							0.1				14.0	0.8			6.7	72.2		0.1	3.6	2.5					2233	Total run[6]	Drucker and Gard, 1967
1967							0.7				29.1	0.3			13.5	44.4			11.4	0.5					1758	Total run[6]	Drucker, 1968
1968			0.1			0.1	5.2			0.1	51.7	2.2			11.0	23.4		0.1	5.9	0.3					1702	Total run[6]	Drucker, 1970
1969			0.2				1.6				47.9	3.5			11.4	31.8			2.8	0.7					995	Fall run	[7]
1970						0.3	0.7			0.4	45.6	1.5			9.4	41.0		0.2	0.9						1054	Total run	Blackett and Davis, 1971
1971							1.3			2.1	41.0	0.2			45.4	9.1			0.8						471	Total run	Blackett, 1973
1972																											
1973						1.0	1.7			1.0	60.1				21.3	11.7			2.7				0.3		291	Spring run	ADFG, Kodiak
1974						1.9	1.3				45.6	1.3			31.0	7.6			11.4						158	Spring run	ADFG, Kodiak
1975			0.5			0.5	3.4			1.0	5.4	3.4			20.6	60.3	2.5		2.0	0.5					204	Spring run	ADFG, Kodiak
1976			0.6			12.8	13.4				33.1	0.6			4.1	32.6			2.3	0.6					172	Spring run	ADFG, Kodiak
1977			1.5			3.9	3.6			3.0	66.3				13.7	4.8			3.3						335	Spring run	ADFG, Kodiak
1978			0.4			2.6	9.4			5.7	52.1	0.4			26.0	1.1			2.3						265	Spring run	ADFG, Kodiak
1979																											
1980						5.5	1.5			11.0	24.8				55.2				2.0							Total run[3]	White, 1985
1981						1.8				7.8	47.8	0.9			24.0	12.2			5.5							Total run[3]	White, 1985
1982						2.8				3.2	39.9	0.4			48.8	1.2			3.7							Total run[3]	White, 1985
1983						1.3	6.6			2.8	67.3	0.1			21.0	0.8			0.1							Total run[3]	White, 1985
1984						1.6	7.3			2.2	54.3	1.0			15.6	16.5			1.5						1134	Total run[3]	White, 1985
1985			0.1			1.2	3.3			1.1	65.3	0.9			9.0	17.4			1.4						2336	Total run[3,6]	Barrett and Nelson, 1995
1986			tr		0.1	0.4	0.7			0.3	52.7	0.5			20.1	16.9		tr	8.4						1383	Total run[3,6]	Barrett and Nelson, 1995
1987	tr	0.1			0.4	1.3	2.5			2.8	47.6	0.6			29.7	7.9		0.1	7.1						3086	Total run[3,6]	Barrett and Nelson, 1995
1988						0.7	2.4			2.3	51.7	0.5			27.5	9.3		0.1	5.6						2446	Total run[3,6]	Barrett and Nelson, 1995
1989	tr	0.1			0.1	3.1	0.3			3.3	46.9	0.1		tr	35.8	6.8			3.6						2739	Total run[3,6]	Barrett and Nelson, 1995
1990		0.3			0.5	0.9	0.3			1.5	45.1	0.4			35.3	10.9		0.2	4.5						2959	Total run[3,6]	Barrett and Nelson, 1995
1991		0.2	tr		0.8	1.2	0.4		tr	1.2	38.5	0.5			33.7	17.6		0.1	5.9					tr	2948	Total run[3,6]	Barrett and Nelson, 1995
1992		0.2	0.2		0.1	0.7	0.8			0.5	21.6	2.2			14.5	52.3		0.1	6.7	0.1					2746	Total run[3,6]	Barrett and Nelson, 1995
1993		0.4	0.1		0.4	1.1	2.2			1.0	23.8	1.7		tr	5.3	53.5		0.1	10.1	0.2		tr	tr		3252	Total run[3,6]	Barrett and Nelson, 1995
1994		0.8	0.1		0.6	3.0	0.6			1.3	37.9	1.1			9.7	36.0	tr	0.1	9.3	0.2		tr	0.2		2973	Total run[3,6]	Barrett and Nelson, 1995
1995		0.1	0.5		0.3	2.7	1.6			3.9	41.9	0.8			21.2	20.0		tr	6.9			0.1	0.1		2545	Total run[3,6]	Nelson and Swanton, 1996

Table 4-1 (cont.)

Percentage occurrence of age groups of Karluk River sockeye salmon runs, 1916–2010.[1]

	Age groups																										
	2_1	3_1	3_2	3_3	4_1	4_2	4_3	4_4	5_1	5_2	5_3	5_4	5_5	6_2	6_3	6_4	6_5	7_3	7_4	7_5	8_3	8_4	8_5	9_5	Sample		Data source
	0.1	0.2	1.1	2.0	0.3	1.2	2.1	3.0	0.4	1.3	2.2	3.1	4.0	1.4	2.3	3.2	4.1	2.4	3.3	4.2	2.5	3.4	4.3	4.4	size	Remarks	(taken or adapted from)
1996		tr	0.2		tr	1.3	1.3			11.0	42.9	0.9		0.1	19.3	12.8		tr	9.2	0.7		tr	0.4		1204	Spring run	ADFG, Kodiak
"			0.3			0.8	1.3			1.7	66.6	0.9		tr	10.3	15.7			2.4	0.2			tr		1340	Fall run	"
1997			0.3		0.1	0.9	4.7			3.4	13.6	3.9			33.0	21.0	0.2	0.1	18.3	0.2			0.4		1199	Spring run	ADFG, Kodiak
"			tr		0.7	0.8	3.9			2.8	13.0	1.1		tr	43.6	19.4		0.1	14.2	0.2					1410	Fall run	"
1998			0.1			2.4	2.0			2.1	61.4	0.6			11.6	15.8		tr	3.3	0.7					1747	Spring run	ADFG, Kodiak
"		0.2			0.2	3.6	0.6			1.7	60.1	0.2			11.1	20.2		0.1	1.9	0.1			tr		1185	Fall run	"
1999						4.0	2.3			7.2	51.3	0.3			22.3	6.1		0.1	6.4				tr		1543	Spring run	ADFG, Kodiak
"		0.1	0.1		0.3	4.9	0.9			1.7	61.4	0.1		tr	20.2	7.5		0.1	2.8			tr			1748	Fall run	"
2000						0.4	1.1			5.9	41.6	0.6		0.1	32.6	9.7		0.3	7.6	0.1		tr			1207	Spring run	ADFG, Kodiak
"			0.1			0.5	tr			0.3	53.9	0.8			24.2	16.7			3.6						753	Fall run	"
2001			0.1		0.3	0.6	1.8			0.3	39.5	0.4			38.3	13.0		0.1	5.3	0.3		tr			1259	Spring run	ADFG, Kodiak
"			tr			0.2	2.5			0.1	32.4	0.3			44.8	14.8		0.1	4.7	0.1					1258	Fall run	"
2002			0.1			0.7	3.2			1.1	37.5	0.5			34.5	13.5		0.2	8.4	0.1		0.2			1525	Spring run	Foster and Witteveen, 2003
"	tr					0.1	3.9			tr	57.0	2.2			17.3	16.1		tr	3.3	tr		tr			1571	Fall run	"
2003			0.1			1.9	3.5			0.7	64.4	0.5			16.0	7.7		tr	5.1			0.1			1388	Spring run	Foster, 2004
"		tr	tr			1.6	2.6		0.1	0.2	58.0	0.5			16.9	14.8			5.2			tr	0.1		1870	Fall run	"
2004						1.2	0.5			4.3	54.7	1.3		0.1	21.3	13.2	0.1		3.0			0.2	tr		695	Spring run	Foster, 2005
"					0.5	0.9	tr			1.2	61.2	0.5			11.8	21.8			1.9				0.1		554	Fall run	"
2005			tr			0.6	1.2			0.6	42.1	1.1		tr	36.3	15.2			2.8						1594	Spring run	Foster, 2006
"			tr			0.3	0.6			0.1	57.6	0.3		tr	16.8	22.9			1.4			tr			1742	Fall run	"
2006						1.0	2.4			0.2	45.5	1.2		tr	23.0	16.4			10.2						1210	Spring run	Foster, 2007
"			tr		0.5	0.6	2.2			0.5	23.2	0.7			51.3	9.6			11.5				tr		1605	Fall run	"
2007		0.2			0.1	0.5	1.9			1.5	14.2	0.3			55.7	10.4		0.1	15.1	0.1		tr			1169	Spring run	Foster, 2008
"		tr	tr		0.2	0.3	0.2			0.9	25.4	0.1			42.3	15.8		0.4	14.0	0.1		tr	tr		1933	Fall run	"
2008			0.2		0.1	0.1	0.3			0.8	20.2	0.4		0.1	38.8	7.9		2.1	27.8	0.3		1.0			531	Spring run	Foster, 2009
"		1.2	tr		0.1	0.7	0.2			0.6	14.0	0.8		0.1	54.6	8.8		4.5	13.0			1.4			773	Fall run	"
2009						8.8	1.8			1.4	24.8	6.8		0.1	23.0	23.1	0.9	1.0	7.1		0.1	1.1	0.1		1018	Spring run	Foster, 2010
"			tr			0.1	0.6			0.2	4.6	3.3			4.7	81.7	0.1	tr	4.5	tr	tr	0.1	tr	tr	1247	Fall run	"
2010			0.9		tr	18.6	6.4			3.1	17.3	5.2			6.3	39.4		tr	1.8	0.8					1155	Spring run	Foster, 2011
"			tr			0.5	0.6			0.2	20.1	0.2			2.2	70.7			1.8	3.3			0.2		1255	Fall run	"

[1] A trace (tr) means that the percentage occurrence was less than 0.05% and an x means that the age group was present, but the percentage occurrence was unknown.
[2] Spring (33%) and fall (67%) runs.
[3] Karluk River spawners were included in the samples used for aging.
[4] Anonymous. Adult age composition data. NARA, Anchorage, AK.
[5] Walker, Charles E. 1956. Age analysis of the Karluk red salmon runs, 1922, 1924-1936, and 1952-1955. Unpubl. report. Located at FRI, University of Washington, Seattle.
[6] Total age composition was weighted by size of spring and fall escapements.
[7] Drucker, Benson. ca. 1969. Length frequency distribution by major age group for male and female sockeye salmon in spring, fall, and total escapements to Karluk Lake, 1956-1969. BCF, ABL Unpubl. tables. Located in personal papers of Richard Gard, Juneau, AK.

importance (the long term averages of 6_4 and 6_3 are similar). This ranking was first reported by Gilbert and Rich (1927) during their analysis of scale samples in 1916. Subsequent investigators have corroborated the usual predominance of 5_3 fish, even though 6_4 and 6_3 age groups were the most abundant in some years (Barnaby, 1944; Rounsefell, 1958; Owen et al., 1962; Gard and Drucker, 1965). Considering the years 1916–2009, the 5_3 age group was most numerous in 64 years, the 6_4 group in 12 years, and the 6_3 group in 12 years (Table 4-1). The fourth most abundant age group was 7_4, which occasionally (e.g. 1952) appeared in larger numbers than the 6_3 or 6_4 age groups.

The age composition varied throughout the season in Karluk River sockeye salmon. Gilbert and Rich (1927), in analyzing 1922 scale data, found that the 6_3 group was abundant in the spring run, but diminished as the summer progressed. The 6_4 group was initially present in low numbers, but increased in abundance later in the spring run and especially in the fall run. The 5_3 age group was abundant throughout the season. Further, Rounsefell (1958) reported that older ocean-aged fish (age groups 6_2, 7_3, 7_4, and 8_4) generally returned early in the season, whereas older freshwater-aged fish (age groups 6_5 and 7_5) usually returned late in the season. Exceptions to this generalization were the 8_5, 3_1, and 4_1 age groups.

Long-term changes in freshwater age composition may also have occurred in the Karluk River sockeye salmon. Barnaby (1944) presented graphical evidence that indicated little or no change in ocean age, but a decrease in 3-freshwater fish and an increase in 4-freshwater fish in most of the returns from the 1922 and the 1924–29 escapements. He suggested that a shortage of phosphorus in Karluk Lake might have caused a decrease in phytoplankton, resulting in decreased growth of sockeye salmon juveniles. This reduced growth might have caused the juveniles to remain in Karluk Lake for an extra year. Unless the relationship changed, he predicted that the majority of the fish in the Karluk sockeye run would be 4-freshwater, whereas formerly the 3-freshwater age group was dominant. To test whether or not this trend continued to present times, we regressed the ratio of percentage occurrence of the

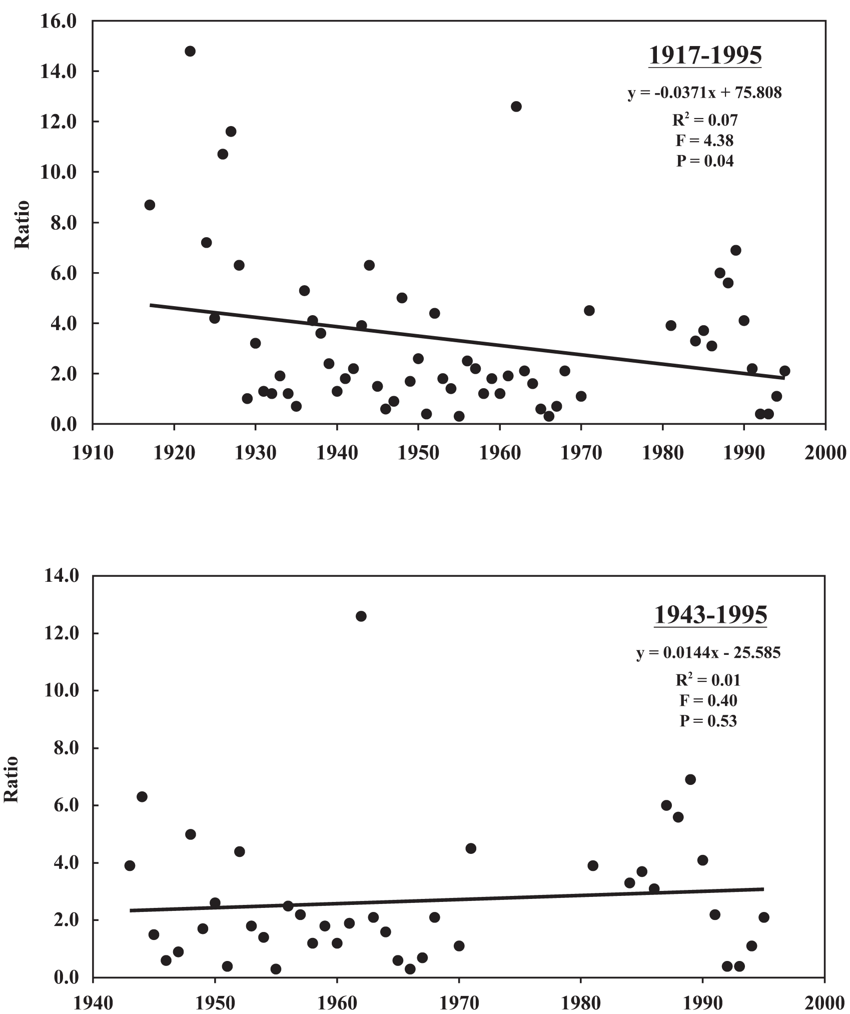


Figure 4-1. Ratio of age group 5_3 to 6_4 in Karluk River sockeye salmon (See Table 4-1 for sources of data by year. Data for 1919, 1921, and 1969 are not included in the analysis because no spring-run samples were taken in those years).

two major age groups (5_3 and 6_4) on year, from 1917 to 1995. Over the entire period, the ratio declined significantly (P = 0.04), but the regression for the 1943–95 period was not significantly different (P = 0.53) from zero (Fig. 4-1). A cursory scan of Table 4-1 suggests that the 6_4 age group may replace the 5_3 group when the latter are in low numbers. It is likely that cycles in freshwater ages may be found that are similar to those reported by Schmidt et al. (1998) for total age.

Size at Return

Size at return is an important life history aspect of Karluk River sockeye salmon. Although lengths of tens of thousands of adult sockeye salmon have been measured over the years, less weight data have been collected. Most references to the weight of adults are from the early years of the fishery, and many of these are anecdotal (Table 4-2). During the 1884–1931 period, Karluk River sockeye salmon averaged about 3.0 kg in weight, with a range of 2.0 to 4.5 kg. Females were somewhat smaller than males, and there may have been a slight downward trend in weight during the period. If we assume that 3.0 kg is a valid average weight (which is questionable), Karluk River sockeye salmon would rank among the heavier North American populations (Burgner, 1991). Chignik sockeye salmon adults averaging 3.2 kg are the largest and Columbia River sockeye averaging 1.6 kg are the smallest.

Sockeye salmon that spend 0 (actually a few weeks) or 1 year at sea are called "jacks," "grilse," or "Arctic salmon." All 0-ocean jacks and most 1-ocean jacks are males. Zero-ocean jacks are in age groups 3_3, 4_4, or 5_5, and they are the smallest returning adults, ranging from only 301 to 338 mm in average mideye-fork length during the 1916–26 period (Table 4-3). The 3_3 and 5_5 types were seen only once, but 4_4's occurred on three occasions. One-ocean jacks (age groups 2_1, 3_2, 4_3, 5_4, and 6_5), with the exception of the rare 2_1's, appear more regularly, with the 4_3's and 5_4's occurring most years. Most of these are small, averaging from 399 to 532 mm in mideye-fork length (Table

Table 4-2
Early references concerning weight of adult sockeye salmon in the Karluk River.

Observer	Year	Avg. weight (kg)	Fish per case	Remarks
Petroff (1884)	1884	4.5		Sockeye salmon not specifically identified.
Bean (1891)	1888	3.2–3.6	13	"Individuals of 15 lbs [6.8 kg] are occasionally seen, but they
	1889	3.2–3.6	12	are uncommon."
Luttrell (1898)	1893		14	
Moser (1899)	1896		12	". . . the early run usually consists
	1897		12	of fish from 14 to 15 and even as high as 17 to the case, but as the season advances they come down to 12 . . . the general average is probably 5½ pounds [2.5 kg] in weight."
Moser (1902)	1900		13.6–13.9	
Kutchin (1904)	1903	2.0		". . . this season the fish were remarkably small . . . commonly they run about 6 pounds [2.7 kg]."
Kutchin (1905)	1904		20	[Normally] "the common average of 13 or 14."
Evermann and Goldsborough (1907)	1903	2.6 males 2.1 females		Males averaged 64.0 cm. Females averaged 60.7 cm.
Baker[1]	1922		13.5–14.5	
Gilbert and Rich (1927)	1925	2.8 5_3 males 2.4 5_3 females		
	1926	2.8 5_3 males 2.5 5_3 females 2.9 6_3 males 2.5 6_3 females 2.8 6_4 males 2.5 6_4 females		
Rich and Ball (1931)	1931		14	Used 14 fish/case to determine number of fish caught from case pack data.

[1]Letter (12 December 1922) from Shirley A. Baker, Assistant Agent, USBF, Cordova, AK, to Commissioner of Fisheries, Washington, DC. Located at NARA, Anchorage, AK.

Table 4-3
Mean mideye-fork length (mm) for male jack sockeye salmon, Karluk Lake, 1916–26 (derived from Gilbert and Rich, 1927).

Year	Male sample size	Mean length by age group for total run						
		3_3	4_4	5_5	3_2	4_3	5_4	6_5
1916	148	—	—	—	—	482	546	—
1917	363	—	—	—	399	—	505	—
1919	45	—	—	—	—	534	—	—
1921	96	—	—	—	—	—	—	—
1922	1175	—	313	338	—	494	502	514
1924	2513	301	322	—	—	482	525	—
1925	2548	—	—	—	—	512	526	—
1926	3523	—	310	—	—	464	524	551
Grand mean		301	315	338	399	495	521	532

4-3). The shortest of the 1-ocean jacks were the 3_2's, which spent only two years in freshwater, and the longest were the 6_5's, which spent five years in freshwater; this shows that some growth occurs during each year spent in freshwater.

Jacks arrive in the Karluk River predominantly toward the end of the run season. A large run of 4_3 jacks is often a harbinger of a large run of 5_3's, as well as a large total run the following year. A good example of this association occurred when a 5.2 percentage occurrence of 4_3 jacks in 1925 was followed by an 81.1 percentage occurrence of 5_3's and a run of 4,918,000 fish in 1926. Similar associations were evident in 1961–62 and 1984–85 (Table 4-1, Figs. 1-2, 1-3).

Two-ocean fish were longer than 1-ocean fish. For the 1916–26 period, total runs of 2-ocean fish from age groups 5_3 and 6_4 averaged 603 and 611 mm in length, respectively (Table 4-4). Fish from age groups 4_3 and 5_4 averaged only 495 and 521 mm in length, respectively (Table 4-3). Growth during the second year at sea averaged 108 mm for the 5_3 fish and 90 mm for the 6_4 fish. It should be pointed out that we don't know how long the 5_3's and 6_4's were one year prior to their capture, and we can only assume they were the lengths of the 4_3's and 5_4's.

Table 4-4
Mean mid-eye-fork length (mm) by major age group for male sockeye salmon in spring, fall, and total runs, Karluk Lake. The 1916–26 data were derived from Gilbert and Rich (1927)[1] and the 1956-69 data were compiled by Benson Drucker.[2]

Year	Sample size	Spring run				Fall run				Total run			
		5_3	6_3	6_4	7_4	5_3	6_3	6_4	7_4	5_3	6_3	6_4	7_4
1916	148	—	—	—	—	606	611	599	—	—	—	—	—
1917	363	—	—	—	—	—	—	—	—	611	635	624	658[3]
1919	45	—	—	—	—	620	658	628	—	—	—	—	—
1921	96	—	—	—	—	619	621	611	—	—	—	—	—
1922	1175	558	—	—	—	592	—	—	—	587	600	588	532[3]
1924	2513	582	—	—	—	617	—	—	—	603	619	612	635
1925	2548	573	—	—	—	614	—	—	—	605	609	612	634
1926	3523	589	612	581	—	624	643	628	—	611	621	619	631
Grand mean		576	612	581	—	613	633	616	—	603	617	611	618
1956	485	501	562	534	581	543	560	547	592	512	561	542	584
1957	841	511	561	513	576	542	572	551	590	522	563	541	578
1958	752	498	541	490	534	547	576	549	574	529	558	535	565
1959	707	526	557	504	547	543	556	547	572	537	557	530	548
1960	1326	510	558	521	551	534	571	548	562	514	558	537	551
1961	475	526	557	520	562	548	576	571	597	532	560	552	571
1962	664	532	561	512	559	553	588	558	—	545	567	522	559
1963	825	520	568	508	552	519	577	531	574	520	575	527	573
1964	489	512	549	507	558	545	538	553	—	518	549	512	558
1965	248	512	553	499	544	542	577	562	570	525	558	548	545
1966	430	524	556	516	554	556	—	569	582	531	556	544	558
1967	553	517	571	526	559	553	593	566	593	531	576	547	564
1968	401	513	567	538	576	548	596	566	628	518	569	552	582
1969	172	—	—	—	—	548	579	554	579	—	—	—	—
Grand mean		516	558	514	558	544	574	555	584	526	562	538	564

[1] From 1916 through 1921 the fish were measured in inches. These were converted to mm by multiplying inches by 25.4. Also, all the lengths measured from 1916 to 1926 were snout-fork lengths. These were converted to mideye-fork lengths using the equation in Hartman and Conkle (1960:55) modified for mm. This was $Y = 23.9 + 0.924X$.
[2] Drucker, Benson. ca. 1969. Length frequency distribution by major age group for male and female sockeye salmon in spring, fall, and total escapements to Karluk Lake, 1956-1969. U.S. Department of the Interior, FWS, BCF, Biological Laboratory, Auke Bay, AK. 27 unpubl. tables.
Copy in the personal papers of Richard Gard, Juneau, AK.
[3] Only one fish was measured.

In like manner, 3-ocean fish were longer than 2-ocean fish. During the 1916–26 period, 6_3 and 7_4 fish averaged 617 and 618 mm in length, respectively (Table 4-4). A comparison of these groups to the 5_3's and 6_4's shows that the 6_3's grew 14 mm and the 7_4's grew only 7 mm during their third ocean year; both growth increments were much less than those for the second ocean year. Taft (1930) also reported little growth of 6_3's and 7_4's during their last year at sea. As pointed out in the previous paragraph, we assume that one year prior to their return the 6_3's and 7_4's were the lengths of 5_3's and 6_4's.

Male sockeye salmon from the Karluk River are usually longer than females. This difference is clearly evident in Figure 4-2 where 2-ocean males were significantly ($P<0.01$) longer than 2-ocean females in 1962 (Gard and Drucker, 1963). However, if there is a large number of jacks such as occurred in 1968 (Fig. 4-3), females may average significantly ($P<0.05$) longer than males. In that year, 8% of the sample was composed of jacks.

Season of return has a profound effect on length. For the 1956–69 period, mean lengths of the major age groups of fall-run males were longer than those for spring-run males (Table 4-4). Similar differences oc-

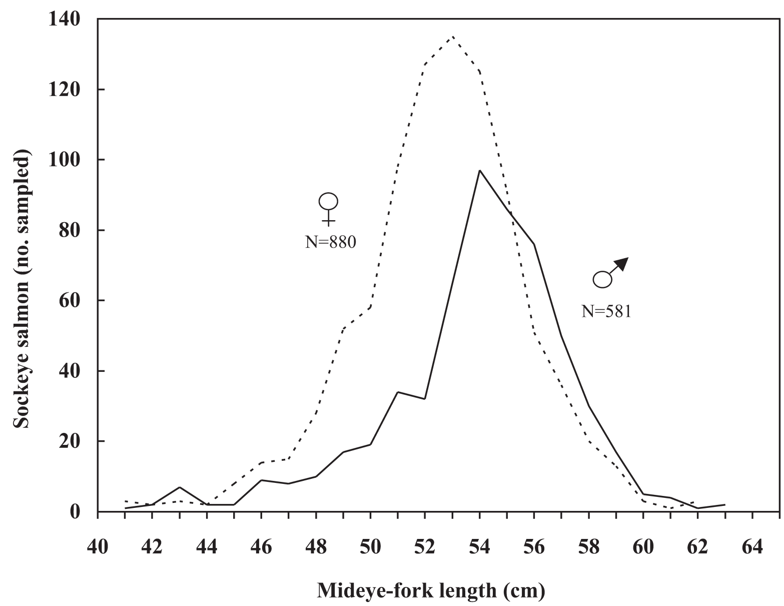


Figure 4-2. Length frequency of 2-year ocean male and female sockeye salmon sampled at the Karluk River weir, 1962 (from Gard and Drucker, 1963).

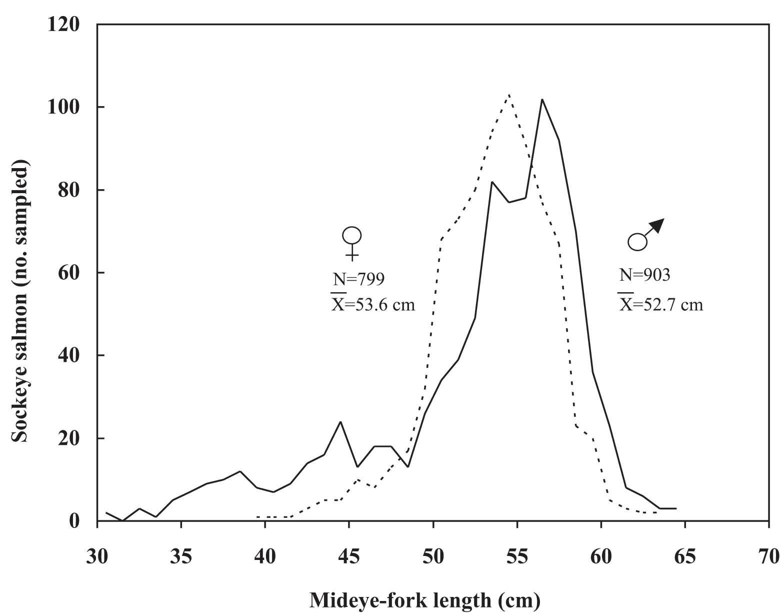


Figure 4-3. Length frequency of male and female sockeye salmon sampled at the Karluk River weir, 1968 (from Drucker, 1970).

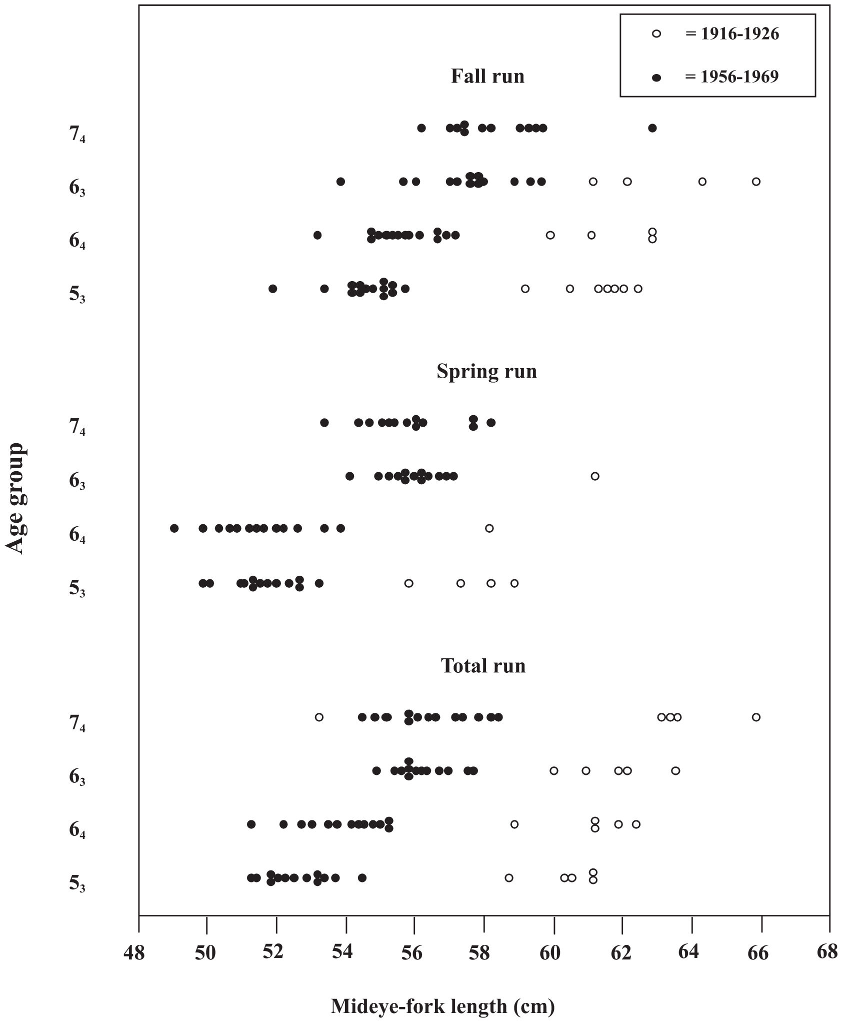


Figure 4-4. Mean mideye-fork lengths by major age group for male sockeye salmon in spring, fall, and total runs to Karluk Lake for individual years of the 1916–26 and 1956–69 periods (data are from Table 4-4).

curred during the 1916–26 period between spring and fall age groups 5_3, 6_3, and 6_4 (Table 4-4).

Gard et al. (1987) found that fall-run females from Karluk River weir and various spawning grounds were significantly (t-test; $P < 0.01$) longer than spring-run females in 1962 and 1963 when the samples were not stratified into age classes. In 1965, when the comparisons were made with 2-ocean females only, fall-run fish were longer than spring-run fish, although the lengths of spring- and fall-run fish from terminal streams did not differ significantly (t-test; $P > 0.05$). This was attributed to small sample sizes.

There appears to have been a substantial decrease in size of Karluk River sockeye salmon between the 1916–26 period and the 1956–69 period (Table 4-4). The grand mean lengths of the major age groups decreased a minimum of 54 mm in the total run of 7_4's, to a maximum of 77 mm in the total run of 5_3's. There was no overlapping of mean lengths for individual years although the single 7_4 fish measured in 1922 was shorter than the mean for any 7_4 sample from the more recent period and may have been an error. These differences are quite apparent from the plots of 1916–26 mean lengths (open circles) and 1956–69 mean lengths (solid circles) for the major age groups and runs (Fig. 4-4). In a comparison of average lengths of spring-run Karluk River sockeye salmon from early (1925–41) and recent (1973–95) years, Martinson (2004) also found a size reduction over time. Similarly, Ricker (1982) reported that between 1950 and 1980 most areas of British Columbia registered small decreases in size of sockeye salmon.

The most significant findings concerning the size of returning sockeye salmon adults were: 1) differences in length from various spawning grounds and between spring and fall runs were evidence supporting the existence of subpopulations (see Chapter 5), and 2) size was primarily determined by the length of stay in the ocean. Gilbert and Rich (1927) first showed that fish spending the shortest time in the sea should have the shortest lengths, and fish spending the longest time in the sea

should have the longest lengths, and 3) that size also varied with freshwater age, sex, and from year-to-year.

Sex Ratio

In the past, it has been generally assumed that there should be as many males as females on the spawning grounds to assure fertilization of all eggs. However, Barnaby (1944) reported that in the 1923–33 returns of sockeye salmon to Karluk Lake, the average occurrence of males was only 43% despite a 50% average occurrence of males in the smolt out-migration for the 1925–34 period. Part of this decrease between the smolt and adult stages was attributed to selection of males by a gill-net fishery off the mouth of the river, but part of the decrease was unexplained. With reference to the earlier years of the same data, Gilbert and Rich (1927) concluded that "This is an unusual condition among red salmon races and appears the more remarkable from the fact that, aside from the grilse, every important year class shows a deficiency of males." In fact, a preponderance of females is neither "unusual" nor "remarkable"; Foerster (1968:116) presents a table of sex ratios from eight British Columbia sockeye systems for the years 1950–58 that generally shows an excess of females. We now know that a modest excess of females may not be harmful with respect to degree of egg fertilization because Mathisen (1962) demonstrated that one male can effectively fertilize the eggs of up to 15 females. However, the suggestion by some that "surplus" males be selectively harvested could be detrimental as a surplus of males would help buffer females from bear predation (see Chapter 10) and would increase lake fertilization (see Chapter 7).

A more recent series of data (1956–68) shows a male-dominated sex ratio for six years and a female-dominated sex ratio for seven years (Table 4-5). Hence, there has been a shift from total female dominance to an almost even split between the sexes since Barnaby's period. Usually when males are substantially more numerous than females, as in 1958, 1961, and 1968, jacks are in abundance (Table 4-1).

As we have seen with length, sex ratio is also closely associated with ocean age. Barnaby (1944) reported that the percentage occurrence of males decreases with increased ocean residence with 100% males in the 0-ocean group and only 35–38% in the 3-ocean group. In the 2-ocean group, which includes the usually abundant 5_3's and 6_4's, the percentage occurrence of males ranges from 32% to 62%. This group has the most balanced sex ratio.

Table 4-5
Sex ratios of adult sockeye salmon in the spring, fall, and total escapement, Karluk Lake, 1956–69.[1]

Year	Spring escapement (male : female)	Fall escapement (male : female)	Total escapement[2] (male : female)
1956	1 : 0.96	1 : 0.83	1 : 0.90
1957	1 : 1.04	1 : 0.89	1 : 0.95
1958	1 : 0.93	1 : 1.25	1 : 1.13
1959	1 : 1.23	1 : 0.95	1 : 1.04
1960	1 : 0.91	1 : 0.89	1 : 0.90
1961	1 : 1.10	1 : 1.19	1 : 1.14
1962	1 : 0.87	1 : 0.68	1 : 0.74
1963	1 : 1.20	1 : 1.33	1 : 1.28
1964	1 : 1.27	1 : 0.95	1 : 1.05
1965	1 : 0.86	1 : 0.84	1 : 0.84
1966	1 : 1.73	1 : 0.97	1 : 1.08
1967	1 : 1.00	1 : 0.78	1 : 0.85
1968	1 : 1.26	1 : 1.04	1 : 1.12
1969	[3]	1 : 0.83	[3]

[1] Drucker, Benson. ca. 1969. Length frequency distribution by major age group for male and female sockeye salmon in spring, fall, and total escapements to Karluk Lake, 1956-1969. U.S. Department of the Interior, FWS, BCF, Biological Laboratory, Auke Bay, AK. 27 unpubl. tables. Copy in the personal papers of Richard Gard, Juneau, AK.
[2] Ratios weighted by escapement size.
[3] Weir washed out.

Upstream Migration

Length of time required for the upstream migration of the spring and fall subpopulations of Karluk River sockeye salmon varies markedly. Both groups pass through the fishery off the mouth of Karluk River and enter the river at Karluk Spit (Fig. 1-4) in two large, distinct waves. The vanguard of the early run arrives at the spit in mid May, and the first fish of the fall run arrive there sometime in July depending on conditions. The first 3 km of the river constitute a lagoon and the fish swim through the lagoon and thence up the river proper for another 34 km before reaching Karluk Lake and its spawning grounds.

There is general agreement that spring-run fish require about 7 days to make the passage, but average travel time for the fall run is longer and ranges from 10 to 28 days (Gard, 1973).[3] Reasons why fall-run fish re-

[3] 1) Rutter, Cloudsley Louis. 1903. Field observations by Cloudsley Rutter on his Karluk work of 1903. Unpubl. notes. 48 p. Copy provided courtesy of Mark R. Jennings (Davis, CA) and located in Box 130, Barton Warren Evermann papers, Library Special Collections, California Academy of Sciences, San Francisco, CA.
2) Simon, Robert J., Jack Lechner, Martin F. Eaton, Peter B. Jackson, and Louis A. Gwartney. 1970. Kodiak area management annual report, 1970. ADFG. Unpubl. report. Located at ASA, Juneau, AK.

quire more time than spring-run fish are that 1) pink salmon are abundant in the fall in even years and they impede the progress of the sockeye salmon by their physical presence, and 2) a fairly high flow of water is required to permit salmon to ascend the shallow Karluk River. Sufficient flows are present throughout the spring run because of snow melt, but adequate flows during the fall run require rain, which is sporadic until mid September.

During the early part of the fall run, fish often enter the lagoon, mill around for a few days, and return to the sea apparently to await better conditions. Unlike other salmon, sockeye tend to form schools in the lagoon. After a good rain an entire school of many thousands may head upstream in a group, leaving the lagoon nearly devoid of fish temporarily. The range in fall travel time from 10 to 28 days, reported in different studies, may also be due to fluctuations in rainfall, or it may depend on where in the lagoon the tagged fish are released. Both Gilbert[4] and Barrett and Nelson (1994) found that it requires an average of about 10 days in the fall for salmon to travel from the Karluk Spit area to the lower weir. That distance is essentially the length of the lagoon, which is over 3 km long. Tagged fish released near Karluk Spit will require more time to reach the lake than fish released near the upper end of the lagoon.

Spawners arrive at the upper weir in two large waves, repeating their pattern of arrival at the river mouth. The first fish of the spring run enter the lake in mid May. Daily escapements build to a peak in mid June and decrease to a few fish in mid to late July. The fall run then commences, tops out between late August and late September and declines to a few fish by November. After reaching the lake, the spring-run fish spend 3–5 weeks migrating and maturing before they appear on the spawning grounds, whereas the fall-run fish require only 1–3 weeks. Spring-run fish may spend a longer time in the lake because they are not as mature as fall-run fish when they enter the lake. Timing of the spring run is precise and hence predictable within a few days from year-to-year and timing of the fall run is imprecise and unpredictable as a result of stream flow and pink salmon escapement patterns. More detail is given in Chapter 6. We do not know what routes the groups of spawners take during their migrations from the lake outlet to their respective spawning grounds.

[4] 1) Letter (18 August 1925) from Ray S. Wood to Fred R. Lucas. 2) Letter (11 September 1925) from Ray S. Wood to Fred G. Morton. Both located at NARA, Anchorage, AK.

Sexual Dimorphism

When sockeye salmon arrive at Karluk Spit they are streamlined and silvery. There are no large dark spots on the back or fins, but rather, a fine black stippling. The dorsal surface is greenish blue grading into a darker blue on top of the head. The gums are lightly pigmented. Both sexes are of similar coloration and form, the main difference being that the snout and jaw of the males are somewhat longer than those of the females. At this stage of maturation a Karluk River sockeye salmon has the appearance of a generalized salmonid. Most of the fish entering the lake during the spring run and a few that enter during the fall run appear as described.

As the season progresses, there is a remarkable change in color and form. These changes become evident toward the end of the spring run when a subtle reddening of the body and elongation of the snout and jaw of the males are evident in fish entering Karluk Lake. The rate of change increases during the fall run. By the time the fish from both runs reach the spawning grounds they appear as follows: Males have bright red backs, somewhat darker red sides, and red adipose, anal, and dorsal fins. Their heads and opercula are green. Spawning males acquire a hump between the head and dorsal fin, become laterally compressed, and develop elongate, hooked lower jaws and snouts with enlarged upper teeth. Females have a coloration similar to males except that their sides are darker. The form of females is much the same as at sea, but their abdomens become enlarged and there is a slight elongation of snout and lower jaw.

Fry and smolts have uniform bluish-green backs and silvery sides with 8–12 short, oval parr marks. No dark spots are on the dorsal fin.

Spawning

Spawning Habitat

At least five distinct spawning grounds are used by Karluk River sockeye salmon. These are 1) lateral streams such as Cottonwood and Salmon creeks, 2) terminal streams such as Thumb and O'Malley rivers, 3) lake beaches especially near the mouths of Thumb and O'Malley rivers, 4) Karluk River below the lake outlet, and 5) Karluk Lagoon at the mouth of Karluk River (Figs. 1-4, 1-5). Most lateral streams are short, shallow, narrow, swift, and steep with thin rubble and gravel substrates except in short stretches above their mouths which are similar to terminal streams. Two lateral

Table 4-6
Physical characteristics of representative spawning habitats of sockeye salmon of the Karluk system (from Owen et al., 1962).

Type and location of spawning area	Area utilized (m^2)	Length utilized (m)	Mean gradient (%)	Streamflow (m/sec)	Streamflow (m^3/sec)	Type of gravel
Lateral streams						
Grassy Point Creek	1,363	427	5.26	0.77	0.41	Shallow gravel of all sizes
Cottonwood Creek	2,425	396	4.13	0.35	0.14	thickly interspersed with
Others	12,935	—	—	—	—	rubble and small boulders.
Total	16,723					
Terminal streams						
Upper Thumb, East Fork	26,422	2,865	0.70	0.85	2.23	Uniform fine gravel and sand.
Others	40,719	—	—	—	—	
Total	67,141					
Outlet River (Karluk)	252,845	4,663	0.2[1]	0.55	18.21	Uniform fine gravel interspersed with pockets of sand in lower reaches.
Karluk Lake Beaches	—	—	—	—	—	Rubble, some rocky
Thumb, O'Malley areas	12,542[2]					outcrops.

[1] Mean gradient estimated.
[2] Area utilized estimated.

streams, Little Lagoon and Spring creeks, are so different from the others that they could be considered a class by themselves: Little Lagoon consists of a pond a few meters back from the lake, fed by little streams. Spring Creek is composed of a few interconnected ponds fed by springs and small streams. The terminal streams are longer, deeper, wider, slower, with less gradient than lateral streams and possess thick, gravel substrates. Upper Karluk River is similar to the terminal streams except that it is wider and has a greater volume flow. Beach spawning areas are generally in deeper, slower moving water than tributary or outlet streams and have a rubble substrate. The Karluk Lagoon spawning area is unique in that it is in brackish water near the head of the lagoon. It may be the only sockeye salmon spawning area in the world in brackish water.[5] Finally, there are a few creeks that empty into Karluk River between the lake outlet and the lagoon that accommodate some spawning sockeye salmon. These are Silver Salmon, Katzenjammer, and Barnaby creeks.

Physical data related to spawning are presented in Table 4-6, which is reprinted from Owen et al. (1962). Total spawning area for the Karluk River system is estimated to be 349,251 m^2. Using this area and the 1955–62 average escapement of 334,000, we determined that an average of 9,543 spawners per hectare were accommodated. This density of spawners is much higher than that for Bristol Bay river systems for which comparable data are available. The Kvichak River system with 4,557 spawners per hectare had the second highest spawning density (Burgner et al., 1969, Tables 12, 15). Terminal streams at Karluk Lake have about four times as much spawning area as lateral streams and the upper 4.8 km of Karluk River have three times as much spawning area as do all the tributary streams together (Owen et al., 1962). However, sockeye salmon may not spawn effectively in the lower part of the 4.8 km stretch because the substrate there is seemingly compacted, fine material under the top several cm of gravel.[6]

Timing and Distribution of Spawners

Distribution of spawners in the tributaries was determined by weekly or biweekly stream surveys. In 1963 spawning occurred between about 1 July and 1 November (Fig. 4-5). The peak of the spring run was about 19 July and the peak of the fall run was about 14 September with the midseason low on 15 August. Ninety-one percent of the lateral stream spawners were from the spring run while terminal stream spawners were from both runs. Canyon Creek and O'Malley River accommodated both runs. Upper Thumb River was occupied by the spring run and Lower Thumb River by the fall run. Most of the lake beaches were used by fall spawners. Although the prime beach spawning areas were near the mouths of Thumb and O'Malley rivers, some beach spawning occurred near lateral stream mouths during the spring run. Upwelling usually was present at

[5] Letter (5 January 1994) from Len Schwarz, ADFG, Division of Sport Fish, Kodiak, AK, to Kevin Delaney, ADFG, Division of Sport Fish, Anchorage, AK. Located at ADFG, Kodiak, AK.

[6] Wilmot, Richard L. Auke Bay, AK. 1996. Personal commun.

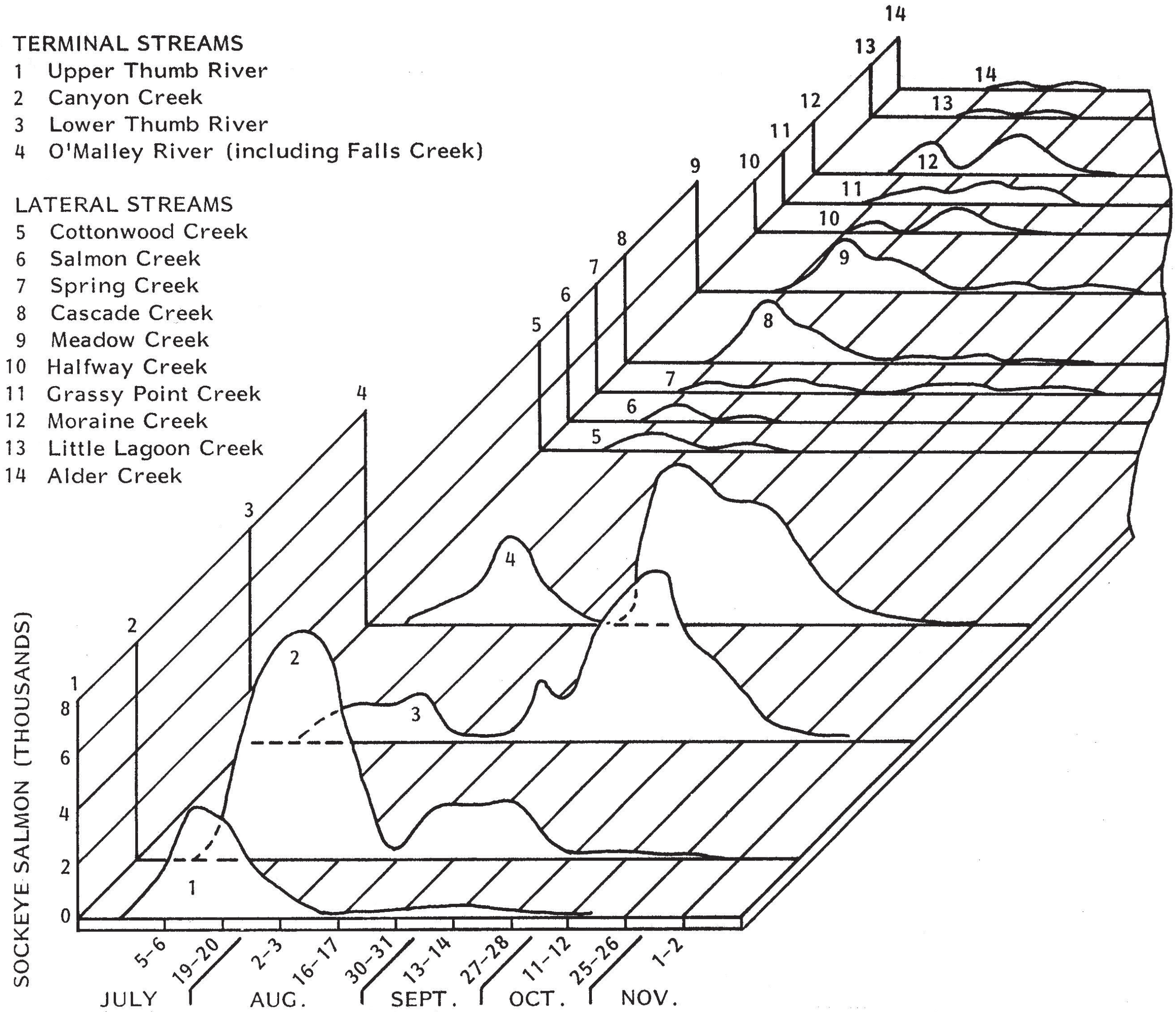


Figure 4-5. Timing and distribution of sockeye salmon on the spawning grounds by weekly stream survey counts, Karluk Lake, 1963 (from Gard and Drucker, 1965).

favored beach spawning sites. Ten percent of the total escapement spawned in Upper Karluk River below the former weir site during late spring and fall runs (Gard and Drucker, 1965). Temporal and spatial distributions of spawners in 1963 were similar to those in 1957, 1958, and 1959 (Owen et al., 1962) and in 1962 and 1964 (Gard and Drucker, 1963, 1966a). This general pattern has existed as far back as 1922.[7]

Spawning Process

After arriving at their natal spawning grounds, mature sockeye salmon initiate the spawning process. The following sequence of events is for Wood River sockeye (Mathisen, 1962), but it generally applies to Karluk River sockeye salmon as well. The female selects a site and starts to dig a nest. She is joined by a male who may help some with the digging and fights off other males who may take up "satellite" positions nearby. Digging is accomplished when the female turns on her side and rapidly flexes her body back and forth. Gravel and sand are lifted from the nest by suction and the current carries the particles away. There are periods of rest when she tests the nest with her anal and pectoral fins. The excavated nest is oblong and measures about 76 × 51 cm with the long dimension parallel to stream flow.

When the nest is ready, the dominant male and female lie side by side quivering with their mouths

[7] Rich, Willis H. 1922 notebook. Location of original notebook unknown; copies at NARA, Anchorage, AK, and ABL Library, Auke Bay, AK.

agape while eggs and sperm are released simultaneously. The spawning act takes 10–12 seconds, and during this period a satellite male may dart in and also release sperm. Fertilization occurs rapidly with an efficiency of nearly 100%. The female then digs on the upstream side of the nest to bury the eggs quickly. She now rests for several hours before excavating another nest nearby and repeats the process until 3–7 nests are completed, each accommodating 500–1,100 eggs. Finally, she covers the batches of eggs with gravel to a depth of 15–23 cm and guards the completed redd until near death.

Longevity of spawners on the spawning grounds was determined at Grassy Point Creek, a lateral stream at Karluk Lake (Gard and Drucker, 1966a). Maximum longevity (time through the weir to time of disappearance) decreased from 14 to 9 days and average longevity decreased from 3.8 to 1.5 days as the season progressed. Salmon entering the creek later in the season were more mature and a progressive decline in longevity would be expected.

Many factors affect the success of spawning, but spawner density may be the most significant. As spawner density increases, egg retention in the bodies of the females, superimposition in the spawning gravels, competition for spawning sites, and mortality of eggs in the gravel also increase. The Karluk River system, with a density of 9,543 sockeye salmon per hectare of spawning area, accommodates the largest known density of spawning sockeye in Alaska (computed from information in Tables 12 and 15 in Burgner et al., 1969).

What is there about Karluk sockeye salmon or the environment they inhabit that permits such a high density? First, the total run is divided into two approximately equal, well-separated runs that extend over a four month period. Second, within each major run there is wave spawning. This may be seen best in the run configurations for the lateral streams (Fig. 4-5). Division into runs and waves within runs ensures that only a portion of the total escapement is on the spawning grounds at any one time. Third, spawners in Karluk lateral streams tolerate each other in closer proximity (<1 m^2 per pair) than do spawners in many other systems. Hartman et al. (1964) suggest that abundant boulders on the bottoms of Karluk lateral streams block the vision of neighboring pairs of spawners, giving them a sense of privacy not present in streams with substrates of uniform gravel. Finally, during years with large escapements, spawners go farther upstream and spawn over a longer period of time than they do in years with smaller escapements.

Although high densities of spawners at Karluk seem to function well during most years, there are limits. In 1926, when there was a huge escapement of 2.5 million sockeye salmon, many females died unspawned. Willis H. Rich observed this event and was so appalled by the waste that he fertilized some eggs from newly-deceased females, planted them in the gravel, and later determined that some of the eggs survived at least the early stages of development.[8]

Fecundity and Egg Size

Fecundity (number of mature eggs per spawning female) is an important life history characteristic. It is an essential element in calculating freshwater survival rates and is used in hatchery operations and in documenting the existence of subpopulations.

Mean fecundity of Karluk sockeye salmon females has been estimated for about 100 years. One of the earliest records was in 1900 when Moser (1902) said that the average fecundity of Karluk hatchery females was 3,000. With reference to a collection made between 5 August and 5 September 1903, Chamberlain (1907:101) stated: "The sockeye carries between 2,500 and 4,000 eggs, an average, perhaps of 3,500." The maximum range of average fecundity for the Karluk system that we found was from 2,145 at Cottonwood Creek to 3,792 at O'Malley River, both counts being obtained in 1965 (Gard et al., 1987). By themselves, the counts mentioned above are of limited value because fecundity varies with size and ocean age of females, with season and year, and with location.

The number of eggs contained in any female is closely related to its length. Therefore, a mathematical expression relating these variables is necessary when fish of different lengths are compared. Smith (1947) and Vladykov (1956) reported that the relationship is curvilinear in salmonids that mature over a wide range of lengths, but since sockeye salmon mature over a narrow size range, a linear equation adequately describes the relationship (Forester and Pritchard, 1941; Rounsefell, 1957; Gard et al., 1987). Therefore, we use linear regression techniques in this report.

That fecundity is related to size of sockeye salmon was reported by Gilbert and Rich (1927): "It is apparent

[8] Rich, Willis H. 1926 notebook. Location of original notebook unknown; copies at NARA, Anchorage, AK, and ABL Library, Auke Bay, AK.

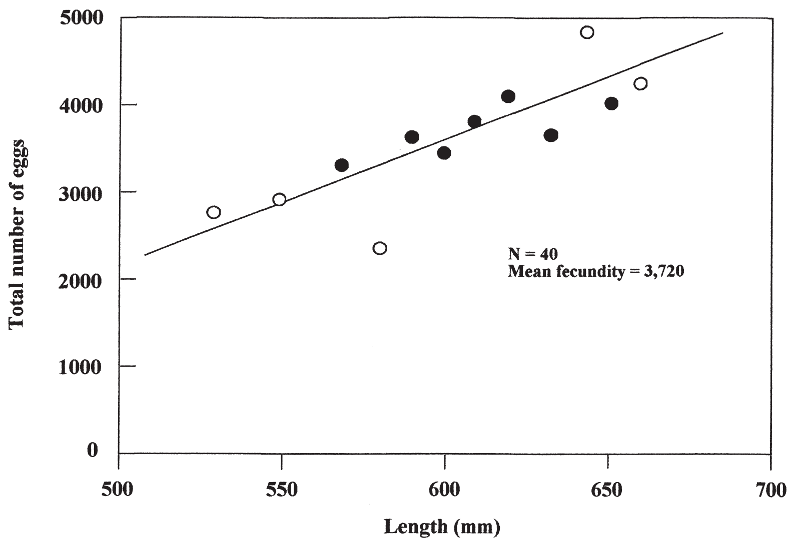


Figure 4-6. Number of eggs in Karluk River sockeye salmon taken on 15 September 1926. Solid circles are mean values for several individuals; open circles are data for single individuals (from Gilbert and Rich, 1927).

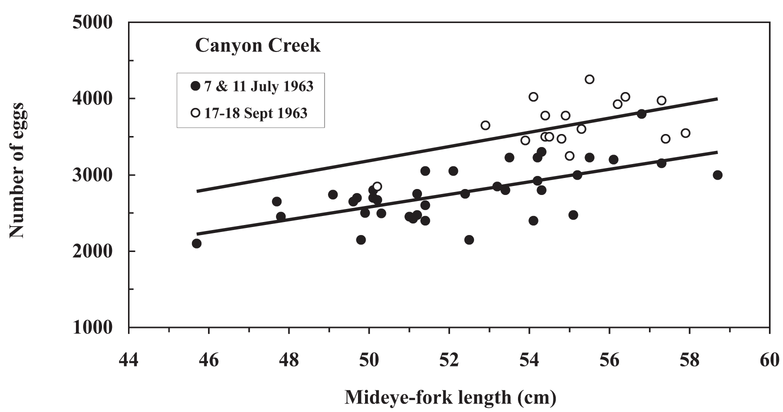


Figure 4-7. Relation of egg content to length of sockeye salmon sampled at Canyon Creek, a terminal tributary of Karluk Lake, July and September 1963 (from Gard and Drucker, 1965).

that the larger females have the greater number of eggs, the relationship being such that a difference of 1 centimeter in the length of the fish is accompanied, on the average, by a difference of 150 in the total number of eggs." Included in their report is the first graph known to us of the regression of total number of eggs on length for Karluk sockeye salmon. Data points and a regression line fitted by eye are shown (Fig. 4-6). Thus, Gilbert and Rich established the format which was followed by subsequent studies of Karluk sockeye salmon fecundity. For example, the regressions of fecundity on length for the 1963 spring and fall samples from Canyon Creek clearly show the dependence of fecundity on length (Fig. 4-7).

To the extent that fecundity is related to size and size is related to ocean age (demonstrated earlier in this chapter), fecundity is also related to ocean age. For example, 2-ocean females are longer and have more eggs than 1-ocean females and 3-ocean females are longer and have more eggs than 2-ocean females (Table 4-7). However, if fecundities of Karluk fish of the same length are compared, younger 2-ocean fish have more eggs than older 3-ocean fish (Rounsefell, 1957:458). He attributed this to the fact that the younger fish are faster growing than the older fish.

Fecundity also varies with season. Between 1963 and 1965 and in 1968, each fall sample of females from the Karluk River weir had a higher mean fecundity and length than each respective spring sample (Table 4-8). Similar differences were evident between spring and

Table 4-7
Reproductive potential of the 1958 escapement at Karluk Lake by age group (Hartman and Conkle, 1960).

Age group	Number of females[1]	Mean mideye-fork length (cm)	Mean fecundity	Potential egg deposition
4_3	814	43.5	1674	1,363,000
5_4	2,471	43.8	1717	4,243,000
5_3	60,872	51.4	2810	171,050,000
6_4	53,601	51.3	2796	149,868,000
6_3	8,695	54.3	3227	28,059,000
7_4	2,186	53.8	3155	6,897,000
Total				361,480,000

[1]Based on a sample of 2108 sockeye salmon from the 1958 experiment.

Table 4-8
Mean mideye-fork length, fecundity, and regression data for sockeye salmon from the Karluk River weir and Grassy Point Creek, a lateral tributary of Karluk Lake (1962, 1963, and 1965 data from Gard et al. (1987), 1964 data from Gard and Drucker (1966a), 1966 data from Drucker and Gard (1967), 1967 data from Drucker (1968), and 1968 data from Drucker (1970)).

Sample site and year	Run	Number of females	Mean mideye-fork length (cm)	Mean fecundity	Intercept (a)	Slope (b)	F[1]
Karluk River Weir							
1963	Spring	44	52.4	2834	−5,791	164.5	
1963	Fall	58	54.3	3435	−7,375	199.1	
1964	Spring	49	52.3	2756	−1,563	82.5	
1964	Fall	70	53.7	3526	−2,399	110.4	
1965	Spring	14	51.5	2811	−6,337	177.5	
1965	Fall	144	54.5	3618	−10,860	265.7	
1968	Spring	23	51.5	2880	−848	72.3	
1968	Fall	48	53.9	3313	−3,530	126.9	
1963–65, 68	Spring						1.52[2]
1963–65, 68	Fall						3.23[3]
Grassy Point Creek							
1962	Spring	30	50.5	2197	−3,879	120.3	
1963	Spring	31	49.1	2225	−4,390	134.7	
1964	Spring	30	48.8	2268	−3,234	113.4	
1965	Spring	30	48.2	2264	−4,633	143.1	
1966	Spring	30	49.3	2332	−2,996	108.1	
1967	Spring	30	50.7	2291	−3,982	123.8	
1968	Spring	30	50.4	2617	−5,001	151.2	
1962–68	Spring						3.94[3]

[1] F statistic from analysis of covariance, which tests the hypothesis that a single line fits all data.
[2] = not significant.
[3] = significant at $P < 0.01$.

fall samples from the spawning grounds (Fig. 4-7), and these differences were used to document the existence of subpopulations (Gard et al., 1987).

Year to year changes in fecundity occur. Fecundity of fall-run samples from the Karluk River weir from 1963–65 and 1968 and of samples from Grassy Point Creek from 1962–68 varied significantly among years (F; $P < 0.01$) (Table 4-8). Also, long-term increases in fecundity of similar-sized sockeye salmon from the Karluk River weir occurred between 1940 and 1965 (Fig. 4-8). In contrast to increase in fecundity, average size of females probably decreased between 1940 and 1965 because, as we have shown earlier, it decreased between the 1916–26 and 1956–68 periods (Fig. 4-4). The reasons for these seemingly contradictory trends are not clear. However, Svärdson (1949) stated that increase in fecundity may be an indication of overfishing and decrease in size is a common response to the exploitation of any animal because the largest individuals are usually the preferred targets.

Egg size within spawning populations in the Karluk River system increases with length of females. The first reference to egg size was by Fassett in 1910 who stated: "The red-salmon eggs at Karluk are reported to be very variable in size, and a big difference is said to be noted between those of the early, or "spring," run and those of the later, or "fall," run. The fall fish are themselves larger,

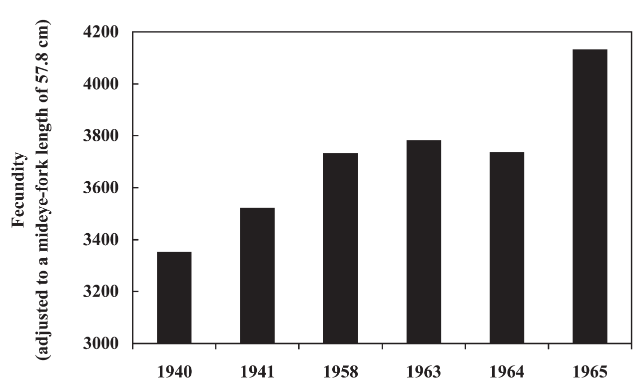


Figure 4-8. Karluk River sockeye salmon fecundity, 1940–65. All data were obtained at a weir in the Karluk River for the spring and fall runs combined. The 1940 and 1941 data are derived from Rounsefell (1957), the 1958 data are from Hartman and Conkle (1960), and the 1963–65 data are from Gard and Drucker (unpubl.).

Table 4-9
Average size of eggs in the largest and smallest sockeye salmon females in spawning ground samples from Karluk Lake, 1965 (Gard, unpubl. data).

Spawning ground	Run	Mideye-fork length (mm)	Number of eggs	Total volume of eggs (cm^3)	Average volume of eggs (cm^3) Largest females	Average volume of eggs (cm^3) Smallest females
Grassy Point Creek	Spring	559	3214	360	.1120	
		413	1414	130		.0919
Meadow Creek	Spring	557	2682	370	.1380	
		461	1905	190		.0997
Cottonwood Creek	Spring	542	2833	350	.1235	
		419	1586	100		.0632
Canyon Creek	Spring	567	3517	390	.1109	
		463	2697	190		.0704
Upper Thumb River	Spring	583	3653	460	.1259	
		482	2425	260		.1072
O'Malley River	Fall	607	4826	500	.1036	
		488	3226	300		.0930
Lower Thumb River	Fall	571	5168	520	.1006	
		493	2363	260		.1100
Thumb Beach	Fall	587	3809	490	.1286	
		477	2764	305		.1103

and have larger eggs, the eggs are more regular in size, and are in greater number."[9] Actual sizes of eggs in the largest and smallest females from several spawning ground samples obtained in 1965 were determined.[10] With the exception of the sample from Lower Thumb River, the largest female in each sample had larger eggs than the smallest female in each sample (Table 4-9). Mathisen (1962) and Bilton (1971) respectively found increased egg size or weight in larger sockeye salmon from the Bristol Bay and Skeena River system streams.

To summarize fecundity relationships for the Karluk River system, mean fecundity varies widely among years and spawning areas with a maximum range of 2,145 to 3,792. Also, fecundity (and egg size) increases with length of fish and between the spring and fall runs. When fish of the same length are compared, younger ocean-age fish are more fecund than older ocean-age fish and there has been a long-term increase in fecundity since 1940.

Egg Deposition

Two expressions of egg deposition are commonly used. One is potential egg deposition (PED) which is the total number of eggs carried into the river system or a segment thereof in the bodies of the females. The second term is actual egg deposition (AED) which is the number of eggs actually deposited in the spawning gravel. To calculate the PED of a given area one must have the number of spawning females, the length frequency distribution of the females, and the equation expressing the regression of number of eggs on length. Usually this information is obtained at a weir. Fecundities for each length or length group are calculated from the regression equation and are multiplied by the numbers of fish in each length group. The sum of these products is the PED.

The method most used today to determine the AED is hydraulic egg pumping. After spawning is completed, many randomly-selected points are successively surrounded by a 0.1 m^2 wire screen and an air/water mixture is pumped into the enclosed gravel dislodging buried eggs which are washed by the current into an attached net. The eggs are enumerated, and an average egg density is calculated and multiplied by the total spawning area giving the AED.

Early investigators were aware of the tremendous number of eggs coming into the Karluk system each year and how few of these survived to the adult stage. Alln[11] calculated that egg to adult mortality was 99.77%. Some of that mortality had to be taking place among the developing eggs in the gravel and Barnaby made the following suggestion:

[9] Fassett, H. C. 1910. Report on the salmon hatchery operated by the Alaska Packers Association on Karluk Lagoon, Kadiak Island, Alaska. Unpubl. report. 25 p. Located at Alaska Historical Collections, Alaska State Library, Juneau, AK.
[10] Gard, Richard. Auke Bay, AK. Unpubl. data.

[11] Memo (6 April 1927) by M. Alln [Possibly Henry D. Aller or Alan C. Taft?] Located at NARA, Anchorage, AK.

> [Concerning the Karluk River sockeye salmon, 1933] By visiting the spawning grounds and digging up nests of eggs laid down during the summer we can find out how these early eggs are developing, how soon they hatch out, when they emerge from the gravel and what natural enemies, if any, they have to contend with at this early stage of their life-history.[12]

There was little response to this suggestion until the 1950s when methods answering two questions were explored. The first question was how many eggs are buried in the gravel of a given spawning area? One method tested was the egg deposition survey which entailed digging holes with a shovel at sites located randomly and catching and counting the excavated eggs in a net. Another method involved the use of an oil drum with the bottom removed. The purpose of the drum was to delineate an area of gravel which was excavated and the eggs enumerated. A third method employed the use of a hydraulic pump and a circular wire screen which has already been described. The first two methods proved to be unsatisfactory, but the egg pumping system gave estimates of the number of eggs in the gravel (AED) as well as ancillary information.

The second question asked was what was the fate of predetermined batches of eggs? To answer that question, various types of egg cartridges, cages containing a known number of live eggs, were buried in the gravel of several tributaries and removed periodically for evaluation. Additionally, adult pens, bottomless cages placed on unseeded gravels and supplied with one pair of mature sockeye salmon each, were installed in four tributaries to determine egg retention, egg deposition, and total eggs recovered from individual females. Considerable data were obtained, but neither method was satisfactory and both were discontinued after 1958 in favor of hydraulic egg pumping of randomly selected points.

Some interesting results were obtained from the various methods used in 1958. Conkle et al. (1959) pumped eggs in several 0.9 m² sample plots located in two lateral streams (Grassy Point and Cottonwood creeks) and one terminal stream (Upper Thumb River). They found that eggs in the terminal stream were buried 23–46 cm deep while those in the lateral streams were only 5–18 cm deep, reflecting the deeper more uniform gravels in the terminal stream. Although their data were not statistically significant at $P = 0.05$ because of small sample sizes, they estimated that 470 live eggs per female were deposited in the terminal stream as compared to 312 and 370 live eggs per female in the lateral streams.

They suggested that the lower number of eggs deposited per female in the lateral streams was due to higher densities of spawners, shallower redds, and greater superimposition. The adult pen studies revealed that egg retention was variable ranging from 0 to 110 eggs per female, and that many more eggs were recovered from about half the pens than were estimated to be in the bodies of the enclosed females. Clearly, eggs were being washed into the pens from spawning activity upstream. In both adult pen and egg pumping studies, survival of eggs that got buried in the gravel was quite high, ranging from 68 to 99%.

The next hydraulic pumping at Karluk Lake was done at Grassy Point Creek in 1964 by Gard and Drucker (1966a) and was continued through 1968 (Drucker, 1970). There were two major differences in the procedure since the initial program in 1958: 1) the area of each sampling point was reduced from 0.9 m² to 0.1 m² and 2) the number of points sampled was increased substantially from 16 to 220 in 1964–66 and 100 in 1967–68 when a stratified sampling scheme was used (for details of methods used see Gard and Drucker, 1966a, b; Drucker, 1968). A weir was installed at the mouth of Grassy Point Creek each year to obtain number and length frequency of females and the regression of fecundity on length so that the potential egg deposition could be calculated. An example of the calculation of the PED in 1964 is shown in Table 4-10.

Table 4-10
Potential egg deposition of sockeye salmon spawning in Grassy Point Creek, 1964 (Gard and Drucker, 1966a).

Length group (cm)	Females in weir sample	Estimated eggs per female	Females spawning	Potential egg deposition
38	1	1108	46	50,968
39	—	—	—	—
40	—	—	—	—
41	1	1447	46	66,562
42	—	—	—	—
43	2	1672	92	153,824
44	2	1785	92	164,220
45	3	1898	138	261,924
46	11	2011	505	1,015,555
47	12	2124	551	1,169,773
48	19	2236	872	1,949,792
49	22	2349	1009	2,370,141
50	14	2462	643	1,583,066
51	3	2575	138	355,212
52	5	2687	230	618,010
53	4	2800	184	515,200
54	1	2913	46	133,998
Total	100	—	4592	10,408,245

[12] Barnaby, J. Thomas. 1933. Work contemplated during the fiscal year 1933. Karluk red salmon investigation, fiscal year, 1933. Unpubl. report. 2 p. Located at NARA, Anchorage, AK.

Table 4-11
Production and survival of sockeye salmon eggs and fry in Grassy Point Creek, 1961-68 (modified from Drucker, 1970, Table 10).

Brood year	Female spawners	PED[1]	AED[2]	PED to AED survival (%)	Average monthly survival rate (2.5 months—PED to AED) (%)	Fry produced	PED to fry survival (%)	AED to fry survival (%)	Average monthly survival rate (7.5 months—AED to fry emergence) (%)
1960	2593	5,699,414[3]	—	—	—	657,370	11.5	—	—
1961	4619	10,152,562[3]	—	—	—	311,773	3.1	—	—
1962	5767	11,938,235	—	—	—	173,472	1.4	—	—
1963	3393	7,475,400	—	—	—	241,925	3.2	—	—
1964	4592	10,408,245	1,487,838	14.3	45.9	410,591	3.9	27.6	84.2
1965	3024	7,096,314	1,053,680	14.8	46.5	451,284	6.4	42.8	89.3
1966	4630	10,525,111	1,299,905	12.4	43.3	344,144	3.3	26.5	83.8
1967	1395	3,133,939	729,643	23.3	55.8	138,646	4.4	19.0	80.1
1968	1895	4,739,059	143,028	3.0	24.6	38,809	0.8	27.1	84.0
						Average	= 4.2		

[1] PED = potential egg deposition.
[2] AED = actual egg deposition.
[3] Based on mean fecundity from 1962.

For the years 1964–68 the survival between PED and AED ranged from 3.0% to 23.3% (Table 4-11). These figures indicated a heavy loss during this period. One or more of the following factors could have caused this loss: retention of eggs by females, washing away of eggs before being buried, superimposition, predation by bears or other animals, and adverse environmental conditions in the gravel. The highest survival (23.3%) was in 1967 when the escapement was restricted to a low 1,395 females. Low spawner density would have resulted in less wave spawning and superimposition and a lower percentage of dead eggs to live eggs (only 6% in 1967 compared to 22–37% during the three previous years). Also, mean egg retention was only 28 eggs per female in 1967 compared to 97 eggs per female in 1968, the only other year for which comparable information was available. Since competition between spawners was minimal in 1967, the females undoubtedly selected the best spawning sites. During 1968, females were also restricted to a low number (1,859), but contrary to expectations, survival from PED to AED was only 3%, the lowest of the five years of study. Drucker (1970) attributed that low survival to extreme predation by subadult brown bears. These bears seemed to prefer to prey on Grassy Point Creek salmon, despite the occurrence of much higher concentrations of salmon in nearby streams.

Incubation

Although considerable effort was expended in the 1950s and 1960s to understand the developmental processes occurring during the incubation period for Karluk sockeye salmon, comparatively little was discovered. Reasonable estimates of actual egg deposition and fry abundance were obtained for some tributary streams, but what occurred between those two points in time was largely conjecture.

It is generally accepted that once the fertilized eggs are in the gravel they are comparatively safe from predators and environmental extremes. Hence survival from AED to fry emergence should be high. Between 1964 and 1968 at Grassy Point Creek, PED to AED survival ranged from 3 to 23% whereas AED to fry emergence[13] survival increased to 19–43% (Table 4-11). Viewed on a monthly basis, average monthly survival rates between PED and AED varied from 25 to 56% whereas comparable survival rates between AED and fry emergence varied from 80 to 89%. Clearly, survival was better after the eggs were in the gravel.

Temperature is usually considered to be the most important environmental factor that determines the rate of development of sockeye salmon embryos. Further, Brannon (1987) reported that temperature units (degree days) required for Fraser River sockeye embryos to develop to the yolk absorption stage varied greatly at different incubation temperatures with many more temperature units required in warmer than in colder waters. This adaptation would tend to synchronize the time of fry emergence from various spawning grounds within a river system so that most of the fry would enter the lake at a time when feeding and survival conditions were optimal.

Hartman et al. (1967) suggested that optimal feeding conditions occurred at Karluk Lake in spring when

[13] Details of fry population estimation are presented in the Fry Emergence and Migration section.

water temperatures rose and plankton bloomed, but Koenings and Burkett (1987b) reported that macroplankter production for the 1980–83 period was highest from September through November. Adults returning to two Karluk tributaries, Canyon and Meadow creeks, in 1962 spawned in two distinct runs and their fry emerged the following spring and summer in two well-separated waves (Gard and Drucker, 1965). There was no tendency for a synchronized emergence of Karluk fry due to a compensatory mechanism operating during the incubation period as was observed by Brannon (1987) for Fraser River fry. If the timing of macroplankton blooms reported by Koenings and Burkett (1987b) occurred consistently over past years, then the late-emerging fry from Canyon and Meadow creeks entered the lake at a propitious time for feeding, but the early-emerging fry did not. Still, the spring run of adults and their early-emerging offspring have existed for at least 100 years, so some selective force other than food supply must also have been operating.

Fry Emergence and Migration

In 1897 Moser (1899) gave a description of sockeye salmon alevin behavior prior to emergence: ". . . . The young with the sac could be seen by taking up a handful of gravel from the bottom. Upon being released they wriggle back in the gravel again." Though he may not have used these terms, what he described was negative phototaxis, positive geotaxis, and thigmotaxis which respectively mean a penchant for darkness, upright orientation on the substrate, and the touch of surrounding gravel. Moreover, if Moser had noted the orientation of the alevins in the gravel with respect to the current, he probably would have seen them facing upstream (positive rheotaxis) (Bams, 1969). These are behavioral responses that pre-emergent fry or alevins exhibit prior to emergence and which must change (or at least weaken) before emergence will occur.

Fry destined to migrate to Karluk Lake originated from many spawning areas. In 1963, fry descending tributary streams were counted at nets near the mouths of Grassy Point Creek (two nets) and Meadow and Canyon creeks (three nets each). The nets were installed in early April and fished until catches became very low. Each night the nets were fished from 1900 to 0700 hours. The nets were emptied every one or two hours, depending on conditions, until 0200 and again at 0700.

To estimate populations, a mark and recapture program was conducted. Samples of fry were periodically stained with Bismarck Brown, released 100 m upstream from the sample sites, and recaptured and enumerated in the nets (Gard and Drucker, 1963, 1965). In addition to the 1963 investigation, fry were also counted in a similar manner in 1961–62 and 1964–68 in Grassy Point Creek, 1962 in Meadow Creek, and 1964 in Canyon Creek. In 1964 fork lengths of fry migrating from Grassy Point and Canyon creeks were also measured.

Timing and direction of sockeye salmon fry migrating to Karluk Lake varied with the situation. Most fry in the lake tributaries migrated downstream at night (Gard and Drucker, 1963; Hartman et al., 1967). By contrast, most fry emerging from the upper Karluk River migrated upstream during the day in large schools near the stream banks. Some may have migrated directly to sea and others may have remained in the river as far downstream as Barnaby Ridge before heading upstream (Raleigh, 1967; Gard et al., 1987).[14] Further, Walker reported that the upstream migrating fry moved in two well-separated waves, the first occurring in May to the early part of June and the second from the latter part of July to the end of August.[15] The diel timing of emergence of Karluk fry is not known, but we assume it was mainly at night because Heard (1964) reported that most sockeye fry in the Brooks River, Alaska, emerged at night and few fry were seen in tributaries of Karluk Lake during the day.

Seasonal timing of fry migration varied among spawning grounds and, as reported earlier, appeared to be related to the timing of spawning of the parents. In 1963, fry migrated from Grassy Point Creek in one wave from early April to late June whereas fry migrated from Canyon and Meadow creeks in two distinct waves between early April and late July (Fig. 4-9). In 1962, the parents of the Grassy Point Creek fry spawned in one wave between July and late August, while the parents of the Canyon and Meadow Creek fry spawned in two waves between early July and October. Apparently the two waves of fry in Canyon and Meadow creeks were derived independently

[14] 1) Bevan, Donald E. 1951. Karluk Lake stream surveys, 1948–1951. FRI, University of Washington, Seattle. Unpubl. report. 45 p.
2) Walker, Charles E. 1954. Karluk young fish study, 1950–1954. FRI, University of Washington, Seattle. Unpubl. report. Both located at FRI Archives, University of Washington, Seattle, WA.

[15] Walker, Charles E. 1954. Karluk young fish study, 1950–1954. FRI, University of Washington, Seattle, WA. Unpubl. report. Located at FRI Archives, University of Washington, Seattle, WA.

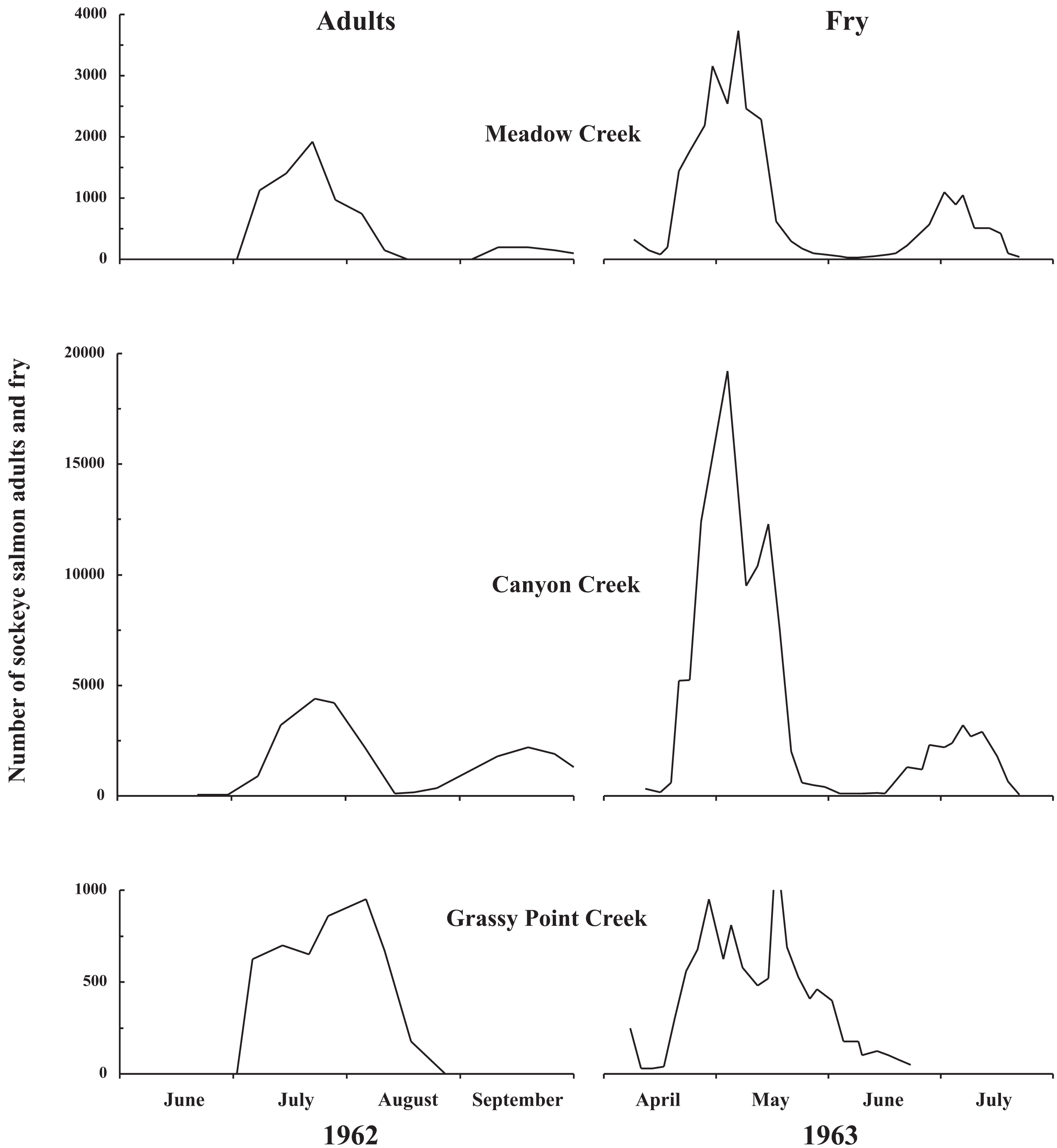


Figure 4-9. Relation between time of sockeye salmon parent spawning in 1962 and time of fry migration in 1963 in three tributaries of Karluk Lake. Fry catches shown are total numbers caught nightly (adapted from Gard and Drucker, 1965, Fig. 20).

from the two waves of spawners. Differences in abundance of parents and offspring in the two waves and differences of about 60 days between the peaks of abundance of the parent and offspring curves support this view (Fig. 4-9). It is not known if the parents of the two groups of fry hatched in the upper Karluk River also spawned in two waves.

In general, the timing and pattern of fry migration have been consistent from year to year. The best example of this is for Grassy Point Creek where beginning and ending dates for the migration varied only a few days during eight years of study (1961–68). Another seasonal phenomenon occurring each year was that as the season progressed and the period of darkness de-

creased, the daily migration period shortened and shifted to later in the evening (Drucker, 1970).

It was likely that most fry in the lateral streams emerged and migrated to the lake during the same night because these streams were relatively short and most stained fry released 100 m upstream reappeared at the nets within four hours. Any fry that did not reach the lake during the night they emerged probably behaved similarly to fry in Hidden Creek, a tributary to Brooks Lake. During the day, those fry remained in protected areas near stream banks in schools, became positively rheotactic, and proceeded toward the lake the following night singly or in small groups while facing downstream (Hartman et al., 1962).

Several fry migrations occurred into or within Karluk Lake. The early wave of fry from the tributary streams entered the lake in April and May, immediately formed schools in littoral areas, and became positively phototactic and rheotactic (Hartman et al., 1967). Rheotactic behavior may have been the mechanism that ensured the fry remained in the lake during the rearing period (Hartman et al., 1962). This early group of fry was soon joined by the first wave of fry from the trunk river in May and early June[16] and by fry hatched above Thumb and O'Malley lakes (Burgner et al., 1969). Apparently, in late July and August most of this assemblage of young-of-the-year fish moved offshore to limnetic areas, as did progeny from beach spawners, as well as late-emerging fry from tributary streams and the Karluk River.[17] Drucker also reported a gradual vertical migration of all ages of juvenile sockeye from surface waters (0–3 m) to subsurface water (3–6 m) between July and September and associated this shift with cooling of surface waters in the fall.[18] Kyle (1990) found similar horizontal and vertical shifts in juvenile populations in Karluk Lake between July and September 1986. Although Pella (1968) found a distinct diel vertical migration of juvenile sockeye in July in Lake Aleknagik, Alaska, this has not been confirmed at Karluk Lake. Finally, Drucker reported that many young-of-the-year migrated from Thumb and O'Malley basins of Karluk Lake to the Weir basin from which the trunk river flows. Navigation by young-of-the-year sockeye within the lake was likely enabled by the utilization of celestial and magnetic cues (Quinn, 1980, 1982a; Quinn and Brannon, 1982).

Some feeding by migrating fry in the spawning streams occurred before they reached the lake. This was especially evident in upper Karluk River where average length of the first wave of fry was 28 mm and that of the second wave was 46 mm.[19] To increase 18 mm in length, the latter group of fry had to be feeding intensively. Chamberlain (1907:31) stated: "Small fingerlings taken in Karluk River May 22 [1903] were feeding on crustacea, insects, and insect larvae." Also, Walker reported for young-of-the-year in upper Karluk River: "Coho fingerling, and to a less extent, red fingerling have been found to contain small reds."[20] Cannibalism, as we will discuss later, may occur among Karluk sockeye.

Feeding by fry has also been documented in tributary streams. Rabe made the following observations at lower Canyon Creek or the O'Malley River in 1956: "Found young of the year (?) stickleback in mouth of dead red migrant in trap."[21] Further, Chamberlain (1907) stated that 11 of 87 fry caught in Spring Creek on 14 July 1903 were feeding and contained insects, larvae, and crustaceans. These fry averaged 41 mm in length and must have been feeding for some time because newly-emerged fry are much shorter. Chamberlain reported catching few fry in other spawning creeks on 16 July and 27 July. There may be a tendency for fry to remain in Spring Creek to feed because it has a series of ponds in which planktonic animals may be in greater abundance than they are in streams lacking ponds.

During their migration to Karluk Lake, sockeye fry, in turn, became the prey of other species. Barnaby counted about one dozen fry in a Dolly Varden stomach from a tributary at the south end of the lake.[22] Further, Dolly Varden 9 to 18 cm long from Thumb, Karluk, and O'Malley rivers contained 6 to 30 sockeye fry.[23] Walker also examined coho fingerlings from the Karluk River that had eaten sockeye fry and concluded that "In summary, it would seem that the [sockeye] fry at the time of

[16] See footnote 15.

[17] 1) Drucker, Benson. ca. 1965. Age, size, abundance and distribution of juvenile sockeye salmon (*Oncorhynchus nerka*) at Karluk Lake, Alaska, 1961–1962. BCF, ABL, Auke Bay, AK. Unpubl. report. 30 p. Located at NARA, Anchorage, AK.
2) Wilmot, Richard L., Carl V. Burger, David B. Wangaard, James W. Terrell, and Robert M. Lichorat. 1983. Karluk Lake studies, progress report. USFWS, Alaska Field Station, National Fishery Research Center, Anchorage, AK (July, 1983). Unpubl. report. Copy from Richard L. Wilmot, ABL, Auke Bay, AK.

[18] See footnote 17.

[19] See footnote 15.

[20] See footnote 15.

[21] Rabe, Fred. 1956 notebook (15 August). Found at NARA, Anchorage, AK.

[22] Barnaby, J. Thomas. 1934 notebook. Found at NARA, Anchorage, AK.

[23] See footnote 15.

emergence and shortly thereafter do undergo considerable predation . . ." Some of the references to Dolly Varden may have included Arctic charr because earlier authors sometimes referred to all charr as Dollies. In a brief food habit study of 18 American mergansers, *Mergus merganser*, and red-breasted mergansers, *Mergus serrator*, Gard found that six individuals from the O'Malley and Karluk rivers contained salmonid fry, some being identified as sockeye salmon.[24] Burgner et al. (1969) mentioned three other species present at Karluk Lake which were known to prey on migrating sockeye salmon fry in other river systems. These were rainbow trout, Arctic terns, *Sterna paradisaea*, and Bonaparte's gulls, *Larus philadelphia*. These species probably ate some migrating sockeye fry at Karluk Lake, but this has never been documented. In any event, migrating sockeye fry at Karluk Lake experienced substantial predation by various species.

Egg to Fry Survival

Survival between potential egg deposition (PED) and fry emergence varied between spawning areas, seasons, and years. For the brood year 1962, PED to fry survival rates of the spring runs to Grassy Point and Meadow creeks (lateral streams) were 1.4% and 2.5%, respectively, whereas survival of the spring run to Canyon Creek (terminal stream) was 8.5% (Tables 4-11, 4-12). Similarly, for the brood year of 1963, the PED to fry survival rates of the spring runs to Grassy Point and Canyon creeks were 3.2% and 11.9%, respectively (Tables 4-11, 4-12). Therefore, survival in terminal streams seems markedly better than it is in lateral streams. As pointed out earlier, terminal streams are slower and deeper than lateral streams and possess a thicker, more uniform gravel bed, characteristics that should provide a superior environment for egg survival. Also, predation by bears on unspawned female sockeye should be less in terminal streams because the deeper water provided better opportunities for escape. Egg to fry survival for the fall run to Meadow Creek for the brood year 1962 was 5.9% while survival for the spring run was only 2.5% (Table 4-12). Better survival for the fall run was expected because bear predation on unspawned adults and superimposition of eggs by subsequent spawners decreased as the season progressed.

In a summary of 37 observations from five sockeye streams in British Columbia and one in Kamchatka,

Table 4-12
Calculated survival rates of sockeye salmon fry in Meadow and Canyon creeks (Gard and Drucker, 1965, 1966a).

Creek (run)	Brood year	Females	PED[1]	Fry	PED to fry survival (%)
Meadow (spring)	1962	6,259	15,993,648	402,971	2.5
Meadow (fall)	1962	528	1,766,104[2]	104,993	5.9
Canyon (spring)	1962	9,456	26,152,260	2,213,200	8.5
Canyon (spring)	1963	11,740	30,974,260	3,676,244	11.9

[1] PED = potential egg deposition.
[2] Estimated figure (see Gard and Drucker, 1965:37).

Foerster (1968:140) calculated an average PED to fry survival of 10.6% (Range 1.8–19.3%). An average of the 13 survival rates for Karluk streams presented in Tables 4-11 and 4-12 was 5.5% (Range 1.4–11.9%). These data are not strictly comparable, but it appears that sockeye egg to fry survival at Karluk is less than that in many other streams. However, this difference could have been the result of differences in methods used or the timing and location of sampling. We have already pointed out the considerable temporal and spatial diversity of egg-to-fry survival rates at Karluk Lake. If the Karluk survival rates had been obtained for the progeny of fall-run sockeye to terminal streams only, the average rate might have been as high as (or higher than) that for the British Columbia and Kamchatka streams.

Life in the Lake

Although there is general agreement that some limiting factor in freshwater is preventing Karluk sockeye from recovering from their present low level, just what that factor is and how it is operating is open to debate. However, a growing cadre of investigators now believe that something relating to the production or availability of food for sockeye juveniles in the lacustrine environment is responsible.

Food and Feeding

Because sockeye salmon are anatomically equipped to eat zooplankton and because Willis Rich recognized the linkage between decomposing adult carcasses and phytoplankton/zooplankton production in Karluk Lake in 1926, subsequent investigators of juvenile foods have concentrated on availability of zooplankton. In

[24] Gard, Richard. 1965. Merganser Food Habits Study, 1965. Unpubl. data. 1 p. Located at NARA, Anchorage, AK.

Table 4-13
Numerical analysis of the net plankton catches for Karluk, Thumb, and O'Malley lakes, 1927 (adapted from Juday et al., 1932, Table 12).

		Average number of organisms per liter of water							
Location and date	Depth (m)	Cladocera	Copepoda	Nauplii	Rotifera	Protozoa	Blue-green algae	Green algae	Diatoms
Karluk Lake Station 1									
19 July	0–125	1.0	8.7	30.5	244.0	11	273	2,928	4,457
31 July	0–125	1.3	1.9	32.3	257.0	1,279	445	28,561	4,802
13 Aug.	0–125	0.7	4.0	47.0	214.0	543	241	1,547	553
24 Aug.	0–125	2.5	12.6	53.4	106.0	729	65	3,679	542
13 Sept.	0–125	2.1	15.3	37.7	29.3	43	9	3,681	226
Thumb Lake									
21 July	0–10	29.5	29.1	24.1	370.0			3,896	1,375,370
3 Aug.	0–10	160.0	33.8	4.6	405.0		31,172		985,825
12 Aug.	0–10	4.2	13.4	0.9	58.2	355			889,000
26 Aug.	0–10	17.8	5.0	0.9	133.0	195			55,134
16 Sept.	0–10	5.0	0.9	1.4	456.0	178		355	309,906
O'Malley Lake									
23 July	0–10	1.2	11.8	6.9	386.0		129		36,040
10 Aug.	0–10	5.0	12.9	5.5	167.0			3,896	502,650
24 Aug.	0–10	2.7	1.8	8.3	147.0	782	7,820	1,564	133,466
14 Sept.	0–10	6.0	1.8	1.0	180.0		1,760	782	145,445

the first such study, Juday et al. (1932) analyzed plankton hauls taken from three locations in Karluk Lake and one location in Thumb and O'Malley lakes. Sampling was done at various depths between mid July and mid September during 1927–30. Results for Karluk station 1 (mid-lake) and for Thumb and O'Malley lakes for 1927 are presented (Table 4-13). The Cladocera were represented in Karluk and Thumb lakes by *Bosmina* and *Daphnia* and in O'Malley Lake by *Bosmina* and *Chydorus.* In all three lakes Copepoda were represented by *Diaptomus* and *Cyclops* and rotifers were the dominant multicellular zooplankter group in all the samples. Protozoans, principally *Epistylis* and *Vorticella,* were found in abundance in Karluk Lake, but in lesser numbers in Thumb and O'Malley lakes. Green algae and diatoms were the dominant elements of the phytoplankton with the blue-green algae playing a minor role. Phytoplankters were most abundant above 20 m where photosynthetic activity was greatest. Although there was considerable variability, most multicellular zooplankter groups occurred in relatively large numbers in July or early August, declined in mid August and increased in late August or September (Table 4-13). No sampling was done after 16 September.

Following Juday et al. (1932) came a remarkable study by Hilliard (1959a) which did not initially receive the attention it deserved. Hilliard conducted a phytoplankton study at Karluk Lake between 20 June 1956 and 22 November 1957 and found that diatoms were the dominant phytoplankters throughout the year, reaching a maximum of 70,975 individuals per liter on 15 October 1956. He also noted, almost as an aside, that one zooplankter, *Cyclops scutifer* (= *C. columbianus*), averaged 0.6 organisms per liter in the summer, but increased to 11 organisms per liter in the fall and early winter, an 18 fold increase! Even more astonishing was that on 8 December 1956 (two days before lake freeze-up), the maximum number of 101 individuals per liter was counted. Juday et al. (1932) reported a 4-year copepod maximum of 37.6 on 7 September 1929. Hence, Hilliard discovered the second annual plankton bloom at Karluk Lake which was one of the major revelations in Karluk research history. As Juday et al. (1932) sampled plankton between 9 July and 13 September only, it is no surprise that Hilliard (1959a:142) concluded: "It is apparent from the available data that sampling over such a limited period (2 months in summer) can give misleading concepts of plankton populations." If Juday et al. (1932) had noted the hints of a second plankton bloom apparent in their data (Table 4-13), they might well have continued sampling into October thus discovering this later bloom at that time.

It was 28 years before the importance of Hilliard's 1959 discovery of a second plankton bloom at Karluk Lake in fall and winter was recognized and corroborated with further sampling (Koenings and Burkett, 1987a, b). These two investigations found that in terms of zooplankton abundance the fall-winter plankton bloom was much larger than the spring plankton bloom (Fig. 4-10). The implications of this discovery of two plankton blooms imposed on early and late fry emergences were enormous and raised many questions such

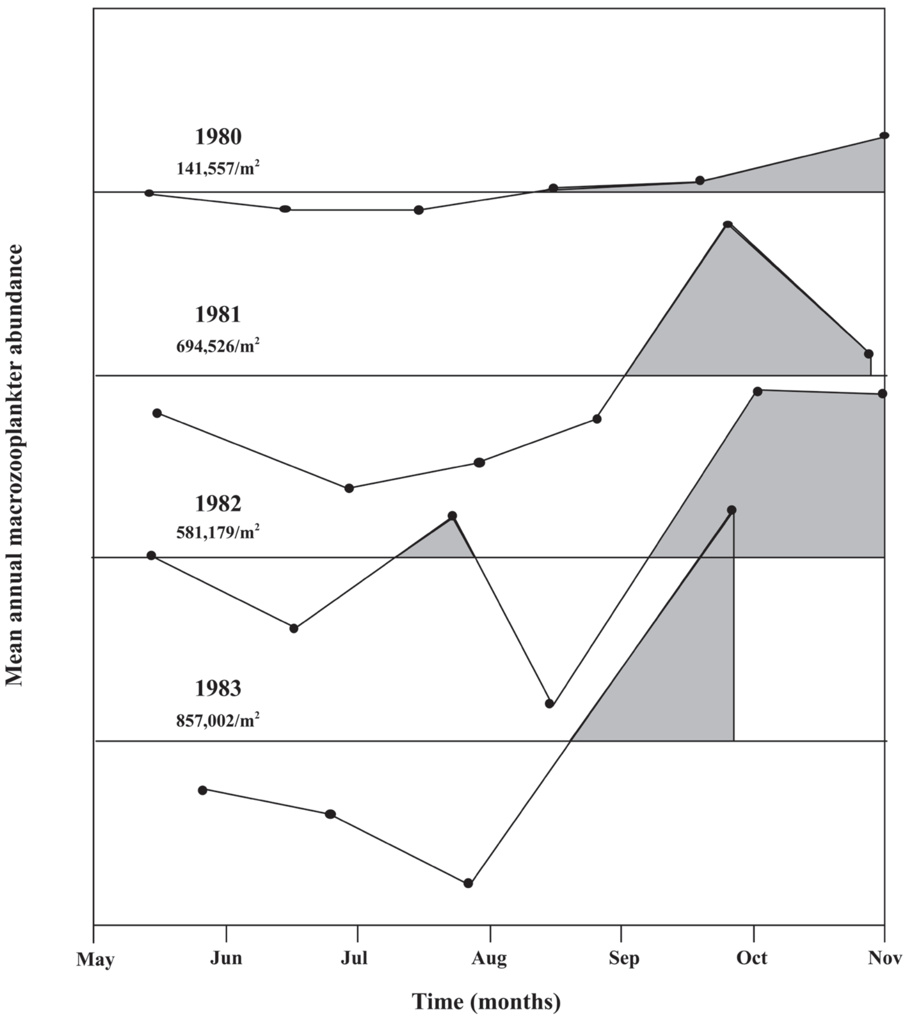


Figure 4-10. The seasonal (May–October) timing of macrozooplankter production at three stations in Karluk Lake over the 1980–83 period (from Koenings and Burkett, 1987b). Solid horizontal lines indicate mean density over the season; individual points within a year show the actual density estimates.

as: Were the two plankton blooms in synchrony with the two fry emergences? Was the larger late plankton bloom the reason why the progeny of fall-run adults survived better than the progeny of spring-run adults? If the plankton blooms and fry emergences were out of synchrony, did this explain why the Karluk runs did not respond to attempts to increase their numbers? The answers to some of these questions were dealt with elsewhere, but the first question to be answered here is: What were juvenile sockeye salmon eating in the lake?

Feeding in the Littoral Zone

We have located few references for juvenile feeding in the littoral zone of Karluk Lake and nearby Bare Lake. On 18 July 1935 Barnaby made beach seine hauls at Camp Island and found "Reds feeding mainly on cladocerans, some copepods, one had flies in its stomach".[25] Further, while discussing stickleback behavior, probably from the littoral areas of Karluk and Bare lakes, Greenbank and Nelson (1959:555) stated: "Juvenile red salmon have been found with sticklebacks in their mouths or stomachs . . ." In August at Bare Lake, Robert F. Raleigh found that on a volumetric basis a sample of juvenile sockeye stomachs contained 55% insects (mostly Diptera), 35% debris, and 10% fish remains (sticklebacks and salmonids).[26] Finally, Nelson (1959) found that the diet of juveniles taken in Bare Lake between May and September 1955 was mainly chironomids. Thus, on the basis of these limited observations, juvenile sockeye salmon in littoral areas of Karluk Lake appeared to eat a combination of zooplankton, insects, and sticklebacks in summer. Chapter 7 provides further details.

[25] Barnaby, J. Thomas. 1935 notebook. Located at NARA, Anchorage, AK.

[26] Raleigh, Robert F. 1956. Kodiak Island red salmon investigations, 1956 field season report. USFWS (31 December 1956). Unpubl. report. 16 p. Located at ABL Office Files, Auke Bay, AK.

Table 4-14

Comparison of percent composition of the major macrozooplankton taxa found in sockeye fry gut contents (Ri) and vertical net tows (Pi) expressed as an electivity index (E). The index has a range of −1 to +1. Positive values indicate active selection, zero indicates random selection, and negative values indicate avoidance or inaccessibility. (Data provided by ADFG Commercial Fish Division, Central Region, Limnology.)

	Bosmina	Ovigerous *Bosmina*	*Daphnia*	Ovigerous *Daphnia*	*Cyclops*	Ovigerous *Cyclops*	*Diaptomus*	Ovigerous *Diaptomus*
Ri	40.81	8.36	3.88	0.02	45.01	0.44	1.46	0.01
Pi	14.64	2.54	4.89	1.06	72.2	0.22	4.45	0
E	0.47	0.53	−0.12	−0.96	−0.23	0.33	−0.51	1

Feeding in the Limnetic Zone

The importance of knowing what juvenile Karluk sockeye eat in the limnetic zone was not recognized until 25 stomachs from the Thumb, O'Malley, and main basins were collected on 21 September 1994 and preserved for later analysis.[27] Because no plankton samples were obtained on that date, mean densities of macrozooplankton seined from O'Malley and main basins on 30 August and 11 October were used for comparison with the contents of the stomachs. The plankton was sampled in the water column with a vertical net tow down to 50 m or the bottom, whichever came first. Percentage composition of the major macrozooplankters in the stomachs and the environment (net tows) were determined and combined as Ivlev's electivity indices. An electivity index is calculated from the equation $E = (r_i - p_i)/(r_i + p_i)$, where r_i = the percentage composition of the prey item in the stomachs and p_i = the percentage composition of the same prey item in the environment. Positive values indicate active selection by the predation, zero indicates random selection, and negative values indicate avoidance or inaccessibility.

Results of the study are summarized in Table 4-14. The most frequent prey species in the stomachs in descending order of importance were *Cyclops, Bosmina,* ovigerous *Bosmina,* and *Daphnia,* whereas the most frequent prey species in the net tows were *Cyclops, Bosmina, Daphnia,* and *Diaptomus*. However, the electivity indices show that ovigerous *Bosmina* were highly selected (0.53) followed by *Bosmina* (0.47), while ovigerous *Daphnia* (−0.96) and *Diaptomus* (−0.51) were avoided or inaccessible. A comparison of weighted mean body size of all prey items from the stomachs and the net tows showed that juveniles, on the average, selected larger prey than existed in the environment. The juveniles ranged in length from 48 to 113 mm. Although four of the juveniles measured over 100 mm in length and were probably capable of consuming smaller fish, no fish were found in the guts.

Cannibalism

Juvenile sockeye are usually plankton eaters, but occasionally they eat fish. Because there are up to five different ages of young sockeye in Karluk Lake at any one time, there has been considerable speculation that older (and larger) individuals may prey on younger (and smaller) individuals. One of the first references to cannibalism at Karluk was by Henry C. Fassett, who inspected the hatchery in 1900, and was quoted by Moser (1902) as stating: "Owing to the cannibalistic tendencies of the larger fry, the young with the egg sac still attached are kept by themselves." Also, Walker, with reference to the Karluk River, reported: ". . . red fingerling have been found to contain small reds."[28] One of the most compelling bits of information suggesting cannibalism in young Karluk sockeye was the tracing through the food chain of unique marine nitrogen isotopes in the bodies of decomposing adult sockeye (Kline, 1992). Specifically, the proportion of marine nitrogen isotopes present in presmolts increased during the fall and winter (Kline, 1993). This change suggested a diet shift from zooplankton to cannibalism on smaller sockeye and possibly predation on sticklebacks as well. Associated with this presumed diet change was a marked increase in size of pre-smolt juveniles. Chapter 7 gives more details. Verification of this hypothesis is presently impossible because there has never been a fall and winter study of juvenile food habits. Such a study is needed if we are to understand the mechanism by which increased escapements would

[27] Data provided by ADFG Commercial Fisheries Division, Central Region, Limnology.

[28] See footnote 15.

Table 4-15

Frequency of occurrence of items in stickleback stomachs from littoral areas of Karluk Lake (adapted from Greenbank and Nelson, 1959, Table 9). Numbers in parentheses are ranges of numbers of organisms per stomach.

	Date							
Food	4 June 1948	7 June 1948	13 June 1948	25 July 1948	7 July 1949	9 Aug. 1949	13 Sept. 1949	Total
Number of stomachs with food	11	23	50	15	68	25	25	217
Number of stomachs with:								
Chironomids	7 (4–14)	10	9		31	2	3	62
Other insects	1				4			5
Copepods *(Diaptomus, Cyclops)*	10 (11–20)	23	22	9 (1–71)	59 (1–276)	24	25	172
Cladocera *(Daphnia, Bosmina)*	3	20		13 (1–182)	31	23	25	115
Ostracods	3 (1)	2	2	5 (1–22)	9 (1–134)	1	1	23
Rotifers	2	13	24		1	1		41
Clams					2			2
Stickleback eggs		1		5 (1–38)	23 (5–58)	1		30

result in larger smolts, smolt outmigrations, and returns of adults.

Potential Competitor Species

Fish species with food habits overlapping those of juvenile sockeye salmon in Alaskan lakes include threespine and ninespine sticklebacks (*Gasterosteus aculeatus* and *Pungitius pungitius*), pond smelt, *Hypomesus olidus*, and pygmy whitefish, *Prosopium coulteri* (Burgner, 1991). Of these, only the threespine and ninespine sticklebacks are present in Karluk Lake and the ninespine stickleback is rare. This leaves the threespine stickleback as the only species that might be a competitor with juvenile sockeye salmon for food or space.

Many biologists have mentioned the possibility of competition for food between sticklebacks and juvenile sockeye salmon in Karluk Lake (Greenbank and Nelson, 1959; Blackett, 1973).[29] Unfortunately, food habits data for juvenile sockeye are scarce, but those which are available appear earlier in this chapter. Hence, stickleback food habits only will be covered here. Barnaby examined some stickleback stomachs captured at Camp Island on 18 July 1935 and reported that they contained stickleback eggs, copepods, and Cladocera.[30] In 1948 and 1949, Greenbank and Nelson (1959) examined 217 stickleback stomachs and found that copepods, Cladocera, and chironomids (larvae and pupae) were the most frequent groups present (Table 4-15). The most important genera of copepods were *Diaptomus* and *Cyclops* as were *Daphnia* and *Bosmina* of the Cladocera. No sockeye fry or eggs were found in the stickleback stomachs. A comparison of stickleback food habits shown in Table 4-15 with juvenile sockeye food habits (Table 4-14) indicates considerable commonality. Although overlapping of food habits does not prove competition exists, it is a prerequisite for that to occur.

To determine if juvenile sockeye salmon and sticklebacks competed for food, Richard Wilmot and associates conducted a study in Karluk, O'Malley, and Thumb lakes from 1985 to 1988.[31] In that investigation, a low-level dam was constructed across O'Malley River to prevent mature sticklebacks from migrating from Karluk

[29] 1) Morton, Mark. ca. 1942. No Title. Unpubl. report. 3 p. Located at NARA, Anchorage, AK.
2) McIntyre, John D. 1980. Further consideration of causes for decline of Karluk sockeye salmon. USFWS. National Fisheries Research Center, Seattle (18 September 1980). Unpubl. report. 29 p. Located at USFWS, National Fisheries Research Center, Seattle, WA.

[30] See footnote 25.

[31] 1) Olson, Robert A., and Richard L. Wilmot. 1989. Karluk Lake sockeye salmon and threespine stickleback studies (1982 to 1988). USFWS, Region 8, Alaska Fish and Wildlife Research Center, Anchorage (29 June 1989). Unpubl. report. 56 p. Copy from Richard L. Wilmot, ABL, Auke Bay, AK.
2) Wilmot, R. L., R. A. Olson, R. R. Reisenbichler, J. D. McIntyre, and J. E. Finn. ca. 1989. Effects of competition with threespine stickleback (*Gasterosteus aculeatus*) on growth of age-0 sockeye salmon (*Oncorhynchus nerka*) in Karluk Lake, Alaska. USFWS, Alaska Fish and Wildlife Research Center, Anchorage, AK. Unpubl. report. 20 p. Copy from Jim Finn, USFWS, Anchorage, AK.

Lake to O'Malley Lake to spawn while allowing free passage of sockeye salmon. A dam was not constructed across Thumb River and therefore sticklebacks had free access to Thumb Lake which served as a control. Growth rates of sticklebacks and young-of-the-year sockeye in the two lakes were determined. Results were that density of sticklebacks in O'Malley Lake was reduced 50% by the weir, and growth of both young sticklebacks and sockeye salmon in O'Malley Lake increased in comparison to growth of these species in Thumb Lake. Wilmot et al. concluded that competition for food existed between sticklebacks and young sockeye salmon in the Karluk Lake system (Chapter 8 provides details).[32]

Predation on Sockeye Salmon in Freshwater

Adult sockeye are known to be the prey of brown bears, red foxes (*Vulpes fulva*), bald eagles, river otters (*Lontra canadensis*), and various species of gulls (*Larus*). The most important of these predators is the brown bear. The percentage of spawners killed by bears in streams with natural escapements ranged from 2% to 74% (average, 43%) in twelve studies (Table 10-2). However, the percentages of bear-killed fish that were unspawned ranged from less than 1% to 31% (average, 11%). Therefore, bear predation on sockeye salmon adults was confined mainly to spawned out fish and had little effect on the succeeding generation (see Chapter 10 for details).

Many animals are known to prey on sockeye salmon eggs during the spawning period at Karluk Lake. Perhaps the most important are the Dolly Varden and Arctic charr whose stomachs often contain sockeye eggs when the adults are spawning nearby. The only question is how many of the eggs would have survived if they had not been consumed by the charrs? Although Moser (1899) reported that charr took eggs as they were deposited, most observers believed that the vast majority of the eggs consumed had washed away before they were buried or were dislodged by late spawners and probably would not have survived (DeLacy, 1941; Foerster, 1968; Morton, 1982). Other animals known to prey on sockeye eggs are coastrange sculpins (Greenbank, 1966), coho salmon,[33] various species of gulls (Morton, 1942),[34] and mallard ducks, *Anas platyrhynchus*.[35] Many of the eggs ingested by birds are drifting eggs although glaucous-winged gulls, *Larus glauceacens*, may walk over nests to dislodge eggs (Moyle, 1966) or peck the bellies of mature female sockeye to stimulate extrusion of eggs (Willson and Halupka, 1995).[36]

During the incubation period, total mortality is high, averaging 71% for the 1964–68 period (Table 4-11). Mortality may have been caused by unfavorable environmental conditions, superimposition, or by intragravel predators such as leeches and oligochaete worms. Heavy infestations of leeches and oligochaetes as well as broken sockeye egg shells were found in egg cartridges buried in Cascade Creek during the 1952–53 incubation period.[37] No one has documented predation by leeches or oligochaetes on sockeye eggs or alevins and it is not known if the embryos were alive or dead when they were presumably eaten. Still, the evidence suggests that predation occurred. Earp and Schwab (1954) reported considerable predation by leeches, *Piscicola salmositica*, on pink salmon alevins in a Washington state salmon hatchery.

Newly emerged Karluk sockeye fry have generally been considered to be vulnerable to predation by several species of birds and fish, the most notable being Dolly Varden and Arctic charr. During the first 50 years of sockeye research a few scattered observations of predation on fry by the two charrs appeared in the literature, accompanied by a great deal of conjecture, until Allan C. DeLacy and William M. Morton examined over 5,000 charr stomachs mainly from Karluk Lake (Tables 9-2, 9-3). DeLacy (1941) and Morton (1982) demonstrated that the two charr preyed little on sockeye fry. For the next 40 years analysis of generally small numbers of charr stomachs from the lake and lake outlet indicated that the lake outlet and the upper Karluk River were likely areas to find significant charr predation on fry if, indeed, it existed. Accordingly, John D. McIntyre, Richard Wilmot, and others examined 1,279 mostly Dolly Varden stomachs collected in the spring between 1982 and 1986 and counted 10,032 sockeye fry (Table 9-3). There was intense predation by Dolly Varden on sockeye

[32] See footnote 31.

[33] Smith, Seymour P. 1927 notebook (27 August). Located at NARA, Anchorage, AK.

[34] 1) Gilbert, Charles H. 1921 notebook. Original at Stanford University Libraries, Department of Special Collection and University Archives, Palo Alto, CA, and a typed summary of Gilbert's survey of Karluk Lake, 8–13 August 1921, at NARA, Anchorage, AK. 2) Morton, William M. 1941 notebook. Original notebook in personal papers of Robert S. Morton, Portland, OR. 3) Freeman, Arthur. 1948 notebook. Original notebook in personal papers of Arthur Freeman, Indianapolis, IN. 4) Gard, Richard. Personal observation.

[35] Gard, Richard. Personal observation.

[36] Armstrong, Robert H. Juneau, AK, Personal commun.

[37] Letter (3 August 1954) from [Phil Nelson] to Carl [Abegglen]. Located at NARA, Anchorage, AK.

fry for several weeks each spring in the upper Karluk River, but this has not been documented elsewhere in the Karluk Lake system or during other seasons. Other predators on sockeye fry were coho and sockeye fingerlings.[38] Also, Gard found that American mergansers and red-breasted mergansers from the upper Karluk and O'Malley rivers contained some sockeye fry.[39]

There is little evidence of predation on sockeye salmon juveniles during their residence in the limnetic waters of Karluk Lake. This may be because few of their most formidable predators, large Dolly Varden and Arctic charr, are present or because observation and sampling methods are more difficult in offshore waters. Examination of a few hundred stomachs of small Dolly Varden taken in the limnetic zone in May showed insects to be the predominant food and sockeye fingerlings to be present in only one stomach.[40] Diving predators, such as Bonaparte's gulls and Arctic terns, probably take some juveniles. Even if the predation intensity is light in the limnetic zone of Karluk Lake, total predation could be substantial because most Karluk juveniles spend 1–3 years in this zone.

Limited quantitative evidence of charr predation on sockeye salmon smolts exists, but there is considerable observational evidence. Morton (1982) examined four Dolly Varden stomachs from the lower Karluk River in 1939 and 1940 that contained 1–10 smolts and Shuman[41] examined one stomach from the lake outlet that contained six smolts (Table 9-3). Many biologists, including the senior author, have witnessed a mass of smolts "boiling" at the river surface immediately upstream from the outlet weir at night while large fish, assumed to be Dolly Varden, cruised below (Hartman et al., 1967).[42] It is likely that the Dolly Varden were feeding on the smolts and the presence of the weir created an unnatural condition that exacerbated the predation. Gard and Drucker (1963) observed no predation by Dolly Varden on sockeye smolts at the lake outlet or below the weir, although both species were present in these locations. However, in upper Karluk River in early June 1984 (nine years after the weir was moved far downstream), large salmonids were observed rushing through schools of smolts and apparently feeding on them.[43] This apparent predation was not verified and quantified by stomach analysis. It should be mentioned that heavy predation of Arctic charr on sockeye smolts has been documented where the Agulowak River enters Lake Aleknagik in the Wood River system (Rogers et al., 1972; Meacham and Clark, 1979). Some 13,000–14,000 charr were estimated to have eaten 3–4 million smolts in 1971. The solution was to confine the charr temporarily in pens during the smolt outmigration. The information presently available for the Karluk River system does not indicate that charr predation on smolts is of the magnitude of that present in the Wood River system. However, only a thorough study of predation by Dolly Varden on smolts in the outlet area and at the site of the present weir near the river mouth when both species are present will determine the role, if any, of a weir and the extent of the predation in the absence of a weir.

Although there is good evidence that young stickleback and young-of-the-year sockeye salmon compete for food and that the young of both species are preyed on significantly by charrs, it is questionable that control of charrs would result in an increased abundance of sockeye. Perhaps, as was suggested by Greenbank and Nelson (1959), charr control would result in an increased abundance of sticklebacks followed by greater competition between sockeye and sticklebacks and a lesser abundance of sockeye. In other words, sticklebacks may act as a buffer against depletion of sockeye by charr predation (see Chapter 9 for details).

Residence Time and Growth

Karluk smolts migrated to sea after spending 1–5 years in fresh water (Table 4-1). This corresponds to 0–4 freshwater growing seasons because the first 10 months were spent in the gravel as eggs or alevins. A 5-year range of residence time in fresh water was unique and may be the longest range known. Only a few fish (age groups 2_1, 3_1, 4_1, 5_1, as designated by the Gilbert-Rich system) migrated to sea after one year and had almost zero freshwater growth. A somewhat larger number (age groups 5_5, 6_5, 7_5, 8_5) went to sea after five years, but the vast majority migrated after three or four years (Table 4-1). Moser (1899) made what may have been the

[38] See footnote 15.

[39] See footnote 24.

[40] USBF. 1938–1943. Monthly report of activities, 1938–1943. U.S. Fisheries Biological Station, Fish and Wildlife Service Biological Station, and Section of Alaska Fishery Investigations, Seattle, WA. Unpubl. report (21 Apr–20 May 1940). Located at NARA, Anchorage, AK.

[41] Shuman, Richard F. 1948 notebook. Located at NARA, Anchorage, AK.

[42] Duncan, T. O. 1955 notebook (21 June). Located at NARA, Anchorage, AK.

[43] USFWS. 1985. Karluk Lake sockeye salmon studies 1984. Part I: Competition, predation, and lake fertility. Part II: Karluk Lake smolt outmigration—1984. Draft. USFWS, Seattle National Fishery Research Center, Alaska Field Station. (January, 1985). Unpubl. report. 39 p. Copies located at ADFG Office Files, Kodiak, AK, and at ARLIS, Anchorage, AK.

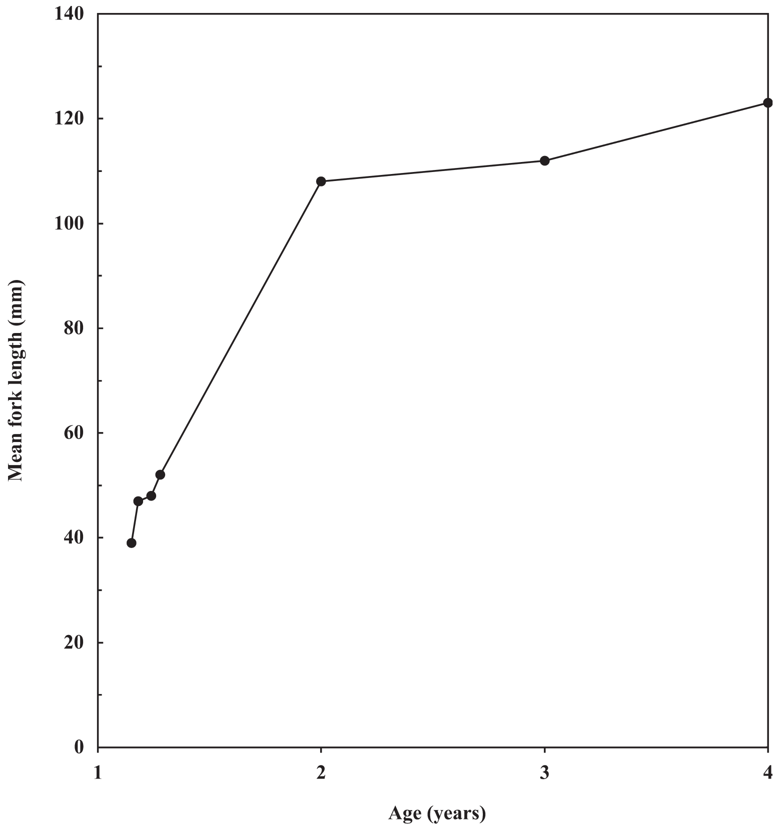


Figure 4-11. Mean lengths of 1-year Karluk sockeye salmon juveniles and 2–4 year smolts from 1962. Lengths of juveniles were obtained from littoral samples (Gard and Drucker, 1963, Fig. 13) and lengths of smolts were obtained from Drucker (1970, Table 21). Age is designated by the Gilbert-Rich system.

first reference to the fact that most sockeye juveniles spent considerable time in fresh water before migrating to the sea: "So far as can be learned, it is a year from this time, [i.e. time of emergence] or the following spring or summer—two years from the time of the arrival of the parent fish—before the young proceed to salt water . . ." Growth influenced duration of time spent in fresh water. Older age groups migrated earlier in the season than younger age groups (Gard and Drucker, 1965) and larger smolts in each age group tended to migrate earlier than smaller smolts (Barnaby, 1944). In addition to age, other factors that determined growth included distribution and abundance of food, water temperature, length of growing season, and density of juveniles.

Although adult sockeye varied greatly in size from about 325–635 mm in mideye-fork length (Gard et al., 1987), newly-emerged fry varied only moderately in size. In 1950, fry seined from littoral areas of Karluk Lake (Island, Long, and Tree points and Thumb Beach) between 31 May and 14 June ranged from 24 to 30 mm in total length.[44] Later that summer, from the shore of Thumb Lake, Walker measured "newly emerged" fry that averaged 26 mm in total length. Walker continued to measure fry in early May 1951 and again reported total lengths from 24 to 30 mm for fry collected from Little Lagoon, Canyon Lagoon, Karluk River, the outlet of Thumb Lake, and lower Thumb River.[45] In April and May 1964, fork length of migrating fry from Grassy Point Creek and the first wave from Canyon Creek averaged 28.9 and 29.8 mm, respectively (Gard et al., 1987). Regardless of natal area, it appeared that newly-emerged Karluk fry varied only 6 mm in length, i.e. from 24 to 30 mm and had an average size of about 27 mm.

A definitive presentation of Karluk sockeye salmon growth in freshwater could not be made with the data available, but an approximation of a growth curve was constructed by plotting mean lengths of 1-year juveniles from littoral areas and of 2–4 year smolts collected in 1962 (Fig. 4-11). The first juvenile sample was measured in late June 1962 and averaged 39 mm in length. The juveniles grew fast for about two weeks, after which there was an apparent pause during July. This temporary flattening of the growth curve was probably the result of the recruitment of small, newly-emerged fry from the late run. Fast growth of juveniles resumed in late 1962. Age 2-, 3- and 4-year smolts for the 1962 outmigration aver-

[44] See footnote 15.

[45] See footnote 15.

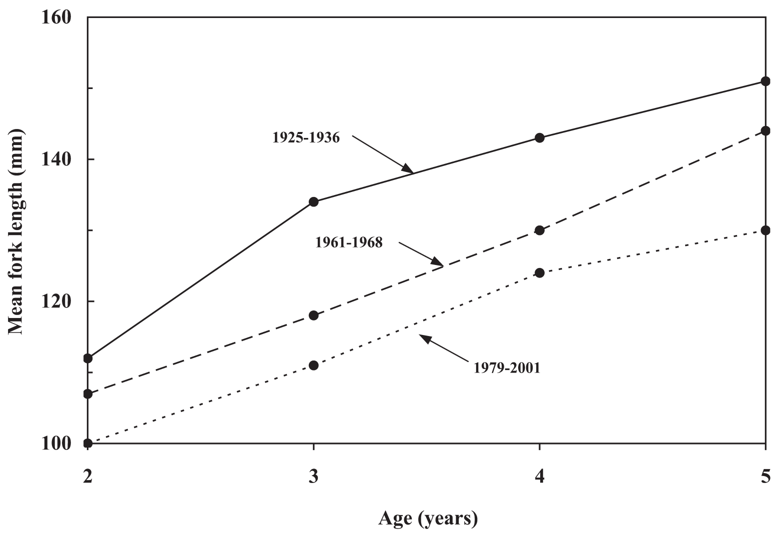


Figure 4-12. Mean length of Karluk Lake sockeye salmon smolts, 1925–2001. Data from Barnaby (1944, Table 27), Drucker (1970, Table 21), Burgner (1991, Table 8), and Schrof and Honnold (2003, Appendix M.12). Age is designated by the Gilbert-Rich system.

aged 108 mm, 112 mm, and 123 mm, respectively. On the basis of these figures, there was a 69 mm growth between age 1 and 2, a 4 mm growth between age 2 and 3, and an 11 mm growth between age 3 and 4. The resulting growth curve was similar to many growth curves as there was a large increase in length between ages 1 and 2 followed by lesser growth between ages 2 and 4.

Earlier in this chapter, we pointed out that adult male sockeye from years 1916–26 were much longer than those from years 1956–69. A similar difference appeared early in the life history of Karluk sockeye. After the 1925–36 period, smolts of all ages and both sexes became progressively shorter during the 1961–68 and 1979–2001 periods (Fig. 4-12). These graphs were constructed by averaging smolt lengths from several outmigrations and, therefore, approximated true growth better than the graph in Figure 4-11 which was based on juvenile and smolt lengths from only one year. However, the mean lengths determined for age groups 2–4 in both Figures 4-11 and 4-12 were too long because the largest individuals in these age groups migrated first and some individuals remained in the lake after each outmigration. Mean lengths of the 5-year smolts in Figure 4–12 were not so biased because all 5-year smolts of the same year class migrated during the same year.

Compared to the expressions of growth described above, a potentially better method would have been back calculating fish sizes at earlier annuli from fish length at time of capture and appropriate scale measurements. With this method, growth of ages 2 through 4 would not have been exaggerated, but finding the proper relationship between body and scale growth was problematical. Barnaby (1932) employed the back calculation method using adult mean lengths and scales from some age groups, but to our knowledge, no one has attempted this recently. A current growth study utilizing back calculation of all age groups and coordinated with a food habits/supply study would be valuable because an accurate expression of freshwater growth and adequate food habits information are not available.

Smolt Outmigration

Before sockeye salmon parr (juveniles) residing in a lake can become functional inhabitants of the sea (smolts), a number of transformations must occur. They must change in color, shape, activity, and, perhaps most importantly, in their ability to tolerate saltwater. Their color becomes more silvery and their bodies become slimmer and more streamlined. Orientation to the current changes from positively rheotactic to generally negatively rheotactic. Osmoregulatory ability changes as their salt glands develop. These changes are brought about by a complex interaction of endogenous and exogenous factors which are summarized in Burgner (1991). Apparently, the primary controlling force in the parr-smolt transformation is an endogenous rhythm in hormone production (Hoar, 1965, 1976; Wedemeyer et al., 1980; Groot, 1982). Environmental factors, especially increasing photoperiods and temperatures, influence the innate hormonal rhythm only after the parr reach a threshold size (Groot, 1982). While these processes are going on, Karluk smolts leave the limnetic areas of the lake, migrate to the trunk river, and continue for 37 km to the sea.

History of Karluk Smolt Observations

Over the past 115 years there have been many references to sockeye salmon smolt migrations in the Karluk River.

Interpretation of some observations was difficult because the term "fry" was used when smolts were probably being observed. Hence, occasionally we were obliged to make arbitrary decisions as to which life history stage was under consideration. For convenience, the 115-year time span was divided into four sections: Early Smolt Observations: 1889–1920, Smolt Observations: 1921–41, Smolt Observations: 1942–69, and Smolt Observations: 1970–2004.

Early Smolt Observations: 1889–1920

Early smolt observations were made from lake and stream banks, supplemented with information from fish acquired with dip nets, traps, and seines. As early as 1889, Bean (1891) reported: "Mr. Charles Hirsch informed me that in March or April the Karluk River is solid full for a whole month of salmon fry going down to sea." Most progeny of spring-run adult sockeye emerge from April to late June and a few of them migrate directly to sea, but the river would hardly be "solid full." Further, Hirsch could not have been observing the early wave of upper Karluk River fry or the smolt run from the lake because neither would have been present in the Karluk River until May. Perhaps the fry observed were not sockeye. Whatever the correct explanation, this observation was of interest because it was the first documentation of young salmon migrating down the Karluk River to the sea.

Several years later, Rutter reported that during May and June salmon fry were abundant in Karluk River from the lake to the estuary.[46] In one seine haul, he identified 40 sockeye fry and 2 fingerlings. On 1 July he set a trap in the river just above the estuary and caught many young of various species including 5 sockeye fingerlings 9–10 cm long. Rutter may have been the first investigator to use traps. Moving down to the estuary on 24 July, Rutter seined 21 sockeye fry and 11 fingerlings 10–14 cm long. The fry may have come from the hatchery which was then operating on the lagoon, and the fingerlings were probably part of the smolt migration from Karluk Lake.

Chamberlain (1907) [reporting on Rutter's 1903 field work] fished a downstream trap at the lake outlet several days in June, apparently during daylight only. Although he caught salmon fry and "parrs" (smolts?), he concluded that there was ". . . but a slight movement of sockeye fry from the lake." He was fishing during the right month to catch the smolt outmigration, but as we now know, most of the smolts migrate at night. Chamberlain also observed many sockeye fry and small fingerlings in the upper Karluk River throughout May and June and dipnetted some fingerlings that averaged nearly 5 cm in length. These fingerlings may have emanated from the second wave of upper Karluk River fry which were feeding in the river prior to migration to the lake.

Passage of 80–130 mm smolts through the lagoon was described by Fassett: "When the migration of these fry [smolt] is on they are seen about the seining beaches on the outside of the spit in tremendous numbers and are hauled in with every sweep of the seine. It is not thought there is much loss on this account, however, as they readily escape through the meshes of the nets."[47] Sporadic visits were made to the Karluk River system from 1911 through 1920, but there were no observations of smolts recorded.

Smolt Observations: 1921–41

Smolt observation and sampling were greatly enhanced by the installation of an adult counting weir in the lower Karluk River just above the lagoon in 1921. This weir, operated under the general supervision of Charles H. Gilbert, was tended each summer season through 1941 and provided a structure above which large numbers of migrating smolts often held temporarily, thus facilitating sampling. A seine was passed around a school of fish, the ends of the seine were pulled to each side of a gate in a holding pen, and the fish were induced to enter the pen by continuing to draw in the ends of the seine (Barnaby, 1944). Between 1921 and 1941 seasonal timing of the smolt outmigration was determined precisely at the weir and samples were collected for weighing, measuring, and age determination. Additionally, during the 1926–36 period between 40,000 and 57,000 smolts seined at the weir were marked annually by the removal of the adipose and one pelvic fin and released below the weir. Recovery of marked fish was done in subsequent years (through 1939) at the canneries and at the weir.

Willis Rich and, subsequently, Joseph Barnaby supervised the smolt marking program. The marking was initiated to serve as a check on age determinations from scales and to enable the calculation of ocean and freshwater mortalities and number of smolts.[48] Further, Taft emphasized that determining smolt numbers was a central goal of the smolt marking program.[49] Although

[46] See footnote 3.

[47] See footnote 9.

[48] USBF. ca. 1930s. Marking experiments. Unpubl. report. 2 p.Located at NARA, Anchorage, AK.

[49] 1) Taft, Alan C. ca. 1928. Karluk red salmon investigations—1927–1928. Unpubl. report. 35 p.
2) Taft, Alan C. ca. 1929. Investigations concerning the red-salmon runs to the Karluk River, Alaska. II. 1927–1928. Unpubl. report. 57 p. Both reports located at NARA, Anchorage, AK.

a smolt population estimate was made for 1926,[50] the main use of the smolt marking was to determine ocean survival (Barnaby, 1944). Gilbert and Rich may not have published the 1926 smolt estimate or produced subsequent estimates because they discovered weaknesses in the method or because they concluded that population estimates for smolt migrations one or more years in the past were not useful.

Smolt Observations: 1942–69

Throughout the 1942–69 period, smolts were collected most years at weirs located at the Portage and at about 300 m below the lake outlet to obtain timing, age, weight, and length data. Smolt age data in the 1930s indicated that there was a change in the amount of time smolts were spending in freshwater and one question under investigation was whether or not the trend was long-term. A second matter to be resolved was the development of a smolt population estimation method that applied to the current year.[51] During the 1950s efforts were made to determine smolt population size by the use of traps or fyke nets in conjunction with marking and recapturing, with minimal success. The most promising of these efforts was in 1958 when eight traps were spaced across the river and fished in a Latin-square design. Unfortunately, the smolts swam between the traps and, although revisions to the design seemed satisfactory, high water washed out the structure before it could be thoroughly tested (Conkle et al., 1959). In 1960 the Latin-square design was developed further and in 1961 a satisfactory estimate of the smolt outmigration was determined. This method with minor modifications was used in determining smolt population estimates through 1969 at the lake outlet weir where the river was 43.9 m wide. Every 3.6 m across the weir was an A-frame, and between every two frames was a trapping site. All fish entering this 3.6-m span were funneled into the winged fyke net. Wire screening was tacked to both sides of the A-frames to prevent smolts from going between the frames and escaping the fyke nets. Two nets were always in position; one net was fishing, the other, with the cod end off, was standing by at the next site to be fished. The Latin-square sampling design was set up to fish randomly 12 sites, each for a 2-hour period each day. At the end of every 12-day period, each site had fished a total of 24 hours. Estimates of the smolt outmigration were computed for each 12-day period by multiplying the total catch by 12. Some modifications to this method were made in 1963 and subsequent years (see Gard and Drucker, 1965 for details). The only serious problem with this method was when the weir washed out, which it did in 1969.

Smolt Observations: 1970–2004

After 1969, smolt observations were made sporadically through 1997. From 1979 to 1982 Sonar was used to enumerate smolts at the "King Hole" located about 4 km below the lake outlet (White 1988b). Chatto,[52] in 1983, and Wilmot and Finn,[53] in 1984, estimated smolt populations using a Canadian fan trap (incorporating mark and recapture) located about 1.5 km below the lake outlet. White (ADFG, ca. 1988), in response to a question concerning both smolt counting methods, said "nothing worked very well," but Chatto thought the fan trap method produced a satisfactory smolt population estimate.[54] Age and length data were also determined at both locations. From 1989 or 1990 to 1996, Steve Honnold and Steve Schrof used hydroacoustic estimates of juvenile populations in Karluk Lake before and after smolt outmigrations to calculate smolt population estimates. This was not successful.[55] The Canadian fan trap was used again in the upper Karluk River in 1991 and 1992 by Lorne White and Steve Honnold to produce acceptable smolt estimates.[56] Finally, in 1997 size and age of smolts were determined at the present weir location just upstream from the lagoon. No smolt investigations were conducted in 1998.

Timing of Smolt Migrations

Seasonal timing of the beginning of smolt migrations through the outlet and lagoon weirs was fairly consistent from year to year. During the 1922–36 period smolts arrived at the lagoon weir between 21 May and 1 June with an average arrival date of 26 May, whereas during

[50] 1) Letter (18 November 1927) from Willis H. Rich, USBF, Stanford University, CA, to C. H. Gilbert, Washington, DC. 2) USBF. 1928. Marking experiments with seaward migrants. Unpubl. report. 5 p. Letter and report located at NARA, Anchorage, AK.

[51] 1) FWS. 1946. Biological investigations in relation to the management of the Karluk sockeye salmon fishery. Unpubl. report. 5 p.
2) Letter (26 February 1953) from Clinton E. Atkinson, Chief, Pacific Salmon Investigations, Seattle, WA, to Regional Director, FWS, Juneau, AK. Report and letter found at NARA, Anchorage, AK.

[52] Chatto, Tony. 1984. Karluk Lake sockeye smolt enumeration, 1983. USFWS, Kodiak National Wildlife Refuge, Kodiak. Unpublish. report. 20 p. Located at Kodiak National Wildlife Refuge files, Kodiak, AK.

[53] Wilmot, Richard, and Jim Finn. Personal commun. 1998.

[54] Chatto, Tony. Kodiak, AK, Personal commun. 1996.

[55] Honnold, Steve. Kodiak, AK. Personal commun. 1998.

[56] See footnote 55.

Table 4-16
Seasonal and diel timing of Karluk smolt migration through the weirs at the lagoon and lake outlet.

Year	First smolt seen	Last smolt seen	Diel timing (%) Day (0400–2000)	Diel timing (%) Night (2000–0400)	Data source
Weir near Karluk Lagoon					
1922	27 May	8 July			[1]
1923	25 May	16 June			[2]
1926	Late May	Late July			[3]
1927	1 June	22 June			[4]
1931	21 May	18 June			[5]
1932	25 May	7 Aug			[6]
1934	21 May	15 June			[7]
1936	28 May	24 June			Bower, 1937
Average	26 May	29 June			
Weir at lake outlet					
1950	21 May				[8]
1958	26 May				[9]
1961	26 May	30 June	22	78	Gard and Drucker, 1963
1962	17 May	22 June	23	77	Gard and Drucker, 1963
1963	18 May	7 July	4	96	Gard and Drucker, 1965
1964	18 May	7 July	8	92	Gard and Drucker, 1966a
1965	15 May	16 July	9	91	Gard and Drucker, 1966b
1966	18 May	2 July	25	75	Drucker and Gard, 1967
1967	18 May	29 June	14	86	Drucker, 1968
1968	17 May	25 June	35	65	Drucker, 1970
1969	25 May				[10]
Average	20 May	2 July	18	82	

[1] Lucas, Fred R. 1924. Summary of red salmon census for the season of 1922 at Karluk Alaska. USBF. Unpubl. report. 5 p. Located at NARA, Anchorage, AK.
[2] Lucas, Fred R. 1924. Report of the red salmon census at Karluk Alaska during the season of 1923. USBF. Unpubl. report. 4 p. Located at NARA, Anchorage, AK.
[3] Hungerford, Howard H. 1926. Report of operations at Karluk Weir (Lower) season of 1926. USBF. Unpubl. report. 4 p. Located at NARA, Anchorage, AK.
[4] Letter (16 June and 2 July 1927) from Ray S. Wood, Foreman In Charge, USBF, Karluk, AK, to H. H. Hungerford, Warden, USBF, Kodiak, AK. Located at NARA, Anchorage, AK.
[5] Wood, Ray S. 1931. Report of the Karluk River weir, 1931. USBF, Karluk, AK. 10 Unpubl. report. Located at ABL Library files, Auke Bay, AK.
[6] Letter (4 Ocotber 1932) from JTB [Joseph Thomas Barnaby], Temporary Assistant, Seattle, WA, to Willis H. Rich, Stanford University, CA. Located at NARA, Anchorage, AK.
[7] Turner, Charles. 1934. Report of operations, Kodiak-Afognak Dist., 1934. USBF. Unpubl. report. 49 p. Located at ABL Library files, Auke Bay, AK.
[8] FWS. 1943-1952. Monthly reports of the Alaska Fishery Investigations. Unpub. reports. Located at NARA, Anchorage, AK.
[9] Conkle, Charles Y. 1958. Karluk Lake field reports (27 April-21 June 1958). BCF, Karluk Lake, AK. 3 Unpubl. report. Located at NARA, Anchorage, AK.
[10] BCF. 1969. Karluk Lake Station 1969 Record Book. Data notebook. Located at NARA, Anchorage, AK.

the 1950–69 period smolts arrived at the outlet weir between 15 May and 26 May with an average arrival date of 20 May (Table 4-16). If there had been no inherent change in timing between the two periods, it took an average of about six days for the migrants to travel the 32 km between the outlet and lagoon weirs at a rate of 5.3 km/d. Withler (1952) reported that sockeye smolts traversed a 13 km stretch of the Babine River at an average rate of 4.2 km/d during a 4-year study. In the Columbia River above Bonneville Dam sockeye smolts averaged 19–40 km/d when they were released 565–645 km above the dam, and 3 km/d when released 32 km above the dam (Anas and Gauley, 1956). Foerster (1968) stated that the speed of travel depends largely on the velocity of the current and the character of the flow, i.e. smolts travel more slowly when they pass through turbulent water, which always occurs at weirs. Many observers, including the senior author, have witnessed large schools of smolts approach a weir, turn and head upstream while moving laterally, and eventually pass quickly through the weir tail first. Upon reaching smooth water they turn downstream and swim with the current.

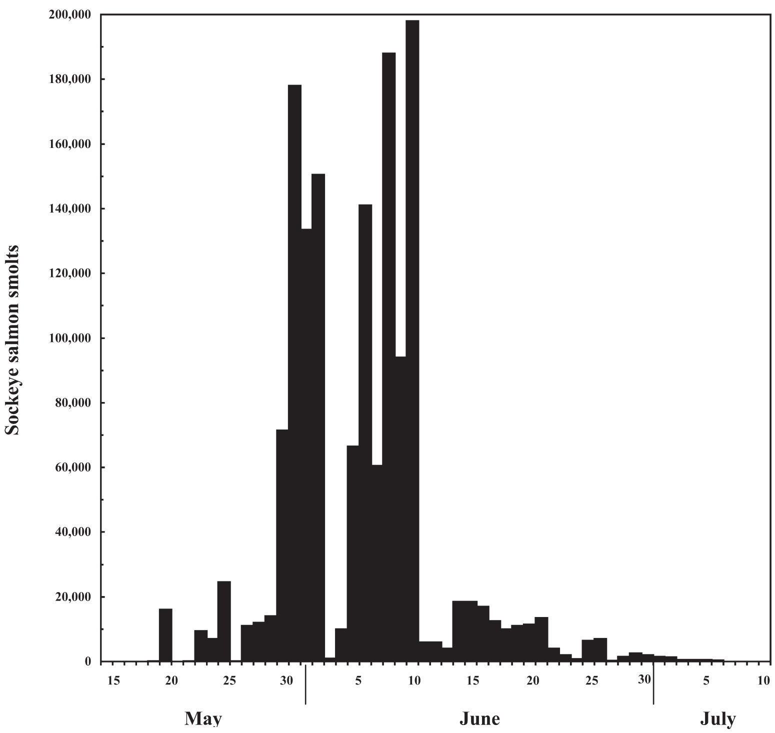


Figure 4-13. Daily estimated sockeye salmon smolt outmigration at Karluk Lake, 1963 (from Gard and Drucker, 1965). Daily totals run from 1900 of one day to 1900 of the next day.

The migration termination dates of Karluk sockeye smolts varied greatly from 15 June to 7 August (Table 4-16). Part of this variability was due to sampling irregularity because sometimes nets were removed immediately after the height of the migration while at other times they were tended for several weeks thereafter. The information we have indicated that smolts migrated in small numbers well into the summer.

A typical smolt migration pattern at the lake outlet is shown in Figure 4-13. In 1963 the smolts arrived at the outlet weir on 18 May, increased by 30 May to high numbers which were maintained through 10 June, and then dropped erratically to very low numbers by 7 July. The tails of the migration pattern were unequal, with the descending tail being twice as long as the ascending tail.

Another way to express seasonal timing of smolt migrations was to determine the date by which 50% of the fish had migrated. The average date so calculated for Karluk smolts migrating through the outlet weir during the 1961–68 period was 1 June. Comparable dates for 16 other sockeye river systems ranged from 25 April at Cultus Lake in the extreme south to 1 July for Taslina Lake in the extreme north (Hartman et al., 1967). A plot of average dates by which 50% of the smolts had migrated against latitude revealed a close correlation between these variables, with the point representing Karluk smolts lying near the middle of the latitudinal and seasonal ranges (Hartman et al., 1967).

Diel timing of departure of Karluk smolts from the lake was mostly at night (Table 4-16). Sixty-five to 96% of the smolts passed through the outlet weir between 2000 and 0400 hours during the 1961–68 period. However, some migration always occurred during the day, the highest being 35% in 1968 (Table 4-16). Kerns (1961), Burgner (1962), Groot (1965), and Hartman et al. (1967) have also reported that sockeye smolts migrated mostly at night.

Changes in age and size of Karluk smolts occurred as the season progressed. Barnaby (1944) reported that older age groups tended to migrate earlier than younger age groups. This was clearly evident when mean age composition of the abundant 3- and 4-year smolts from

Table 4-17
Mean age composition of Karluk sockeye salmon smolt outmigration by seasonal time period, 1962-68.[1]

	Total outmigration (%)			
Age	1st time period (15–29 May)	2nd time period (27 May–10 June)	3rd time period (8–22 June)	4th time period (21 June–15 July)
5	0.5	0.8	0.5	0.0
4	58.9	43.5	21.7	14.9
3	38.8	52.1	74.4	74.4
2	1.8	3.6	3.4	10.4

[1]Compiled from BCF Karluk Lake Station Record books 1962–68 located at NARA, Anchorage, AK.

Table 4-18
Estimated numbers of sockeye salmon smolts in outmigrations from Karluk Lake.

Year	Smolt outmigration	Agency	Sampling location	Method used	Reference
1961	1,694,761	BCF	Outlet weir	Fyke net and Latin square	Gard and Drucker, 1963
1962	1,434,864	BCF	Outlet weir	Fyke net and Latin square	Gard and Drucker, 1963
1963	1,539,599	BCF	Outlet weir	Fyke net and Latin square	Gard and Drucker, 1965
1964	1,561,105	BCF	Outlet weir	Fyke net and Latin square	Gard and Drucker, 1966a
1965	1,469,307	BCF	Outlet weir	Fyke net and Latin square	Gard and Drucker, 1966b
1966	1,080,950	BCF	Outlet weir	Fyke net and Latin square	Drucker and Gard, 1967
1967	1,358,237	BCF	Outlet weir	Fyke net and Latin square	Drucker, 1968
1968	3,641,665	BCF	Outlet weir	Fyke net and Latin square	Drucker, 1970
1979	1,001,000	ADFG	4 km below outlet	Sonar	White, 1988b
1980	1,687,200	ADFG	4 km below outlet	Sonar	White, 1988b
1981	2,041,900	ADFG	4 km below outlet	Sonar	White, 1988b
1982	821,200	ADFG	4 km below outlet	Sonar	White, 1988b
1983	941,500	USFWS	1.5 km below outlet	Fan trap and mark-recapture	[1]
1984	1,074,000	USFWS	1.5 km below outlet	Fan trap and mark-recapture	Schrof and Honnold, 2003
1991	4,700,000	ADFG	1.5 km below outlet	Fan trap and mark-recapture	Holland and McKean, 1992
1992	3,700,000	ADFG	1.5 km below outlet	Fan trap and mark-recapture	McNair and Holland, 1993
1999	1,066,534	ADFG	1.5 km below outlet	Fan trap and mark-recapture	Schrof and Honnold, 2003
2000	1,676,702	ADFG	1.5 km below outlet	Fan trap and mark-recapture	Schrof and Honnold, 2003
2001	3,740,268	ADFG	1.5 km below outlet	Fan trap and mark-recapture	Schrof and Honnold, 2003
2002	1,300,000	ADFG	1.5 km below outlet	Fan trap and mark-recapture	ADFG, Kodiak
2003	2,200,000	ADFG	1.5 km below outlet	Fan trap and mark-recapture	ADFG, Kodiak
2004	2,300,000	ADFG	1.5 km below outlet	Fan trap and mark-recapture	ADFG, Kodiak
2005	1,500,000	ADFG	1.5 km below outlet	Fan trap and mark-recapture	ADFG, Kodiak
2006	1,200,000	ADFG	1.5 km below outlet	Fan trap and mark-recapture	ADFG, Kodiak

[1] Chatto, Tony. 1984. Karluk Lake sockeye smolt enumeration, 1983. USFWS, Kodiak National Wildlife Refuge, Kodiak, AK. Unpubl. report. 20 p. Located at USFWS, Kodiak National Wildlife Refuge files, Kodiak, AK.

the 1962–68 period were compared (Table 4-17). Four-year smolts decreased from 58.9% of the outmigration during the first time period to only 14.9% during the fourth time period, while 3-year fish increased from 38.8% in the first time period to 74.4% in the last time period. The youngest fish sampled (age 2) increased from 1.8% to 10.4% as the season progressed. Data for the 5-year fish were not clear-cut, but not one was found in the latest period. During the outmigration season larger smolts often migrated earliest. This was partly because the older fish that migrated earliest were larger, but even within one year class the larger fish migrated earlier (Barnaby, 1944).

The external stimulus that triggered smolts in the appropriate physiological condition to migrate was primarily increasing water temperature, with its attendant effect on ice breakup. However, wind velocity and direction and photoperiodism may also have been involved (Foerster, 1968; Hartman et al., 1967; Burgner, 1991).

Abundance of Smolts

During the 1961–2006 period estimated numbers of sockeye smolts that migrated from Karluk Lake varied widely from 821,200 in 1982 to 4,700,000 in 1991 (Table 4-18). However, during the first seven years of this period (1961–67) estimated smolt numbers were fairly constant, averaging about 1,500,000 fish (Table 4-18). Then in 1968, the smolt outmigration was estimated to be 3,642,000; this was the result of excellent freshwater survival because the parent generations in 1964 and 1965 were not particularly large. These smolts did not survive well at sea because all age groups were short (Drucker, 1970) and the expected large adult returns in 1970 and 1971 did not materialize (Figs. 1-2, 1-3). Other years of interest were 1991 and 1992 when an estimated 4,700,000 and 3,700,000 smolts, respectively, migrated (Table 4-18). These large smolt outmigrations were probably, in part, the result of fertilization of Karluk Lake between 1986 and 1990 although sockeye populations increased simultaneously in nearby unfertilized sockeye systems (see Chapter 7).

The series of smolt numbers presented here is exceedingly important to our understanding of the life history of Karluk sockeye because it, in conjunction with adult counts, permits us to determine total freshwater and marine survival rates. These will be discussed in subsequent sections of this chapter.

Survival in Fresh Water

Survival between the potential egg deposition and smolt migration stages of Karluk sockeye salmon varied from

Table 4-19
Survival of sockeye salmon at Karluk Lake during the freshwater phase of the life cycle. Brood years 1958-61 are from Gard and Drucker (1966b) and brood years 1962-65 are from Drucker (1970).

Brood Year	Escapement	Potential eggs deposited[1]	Smolts produced	Total freshwater survival (%)
1958	303,914	468,000,000	1,853,000	0.40
1959	493,589	803,000,000	2,001,000	0.25
1960	387,434	682,000,000	1,906,000	0.28
1961	329,596	485,000,000	1,143,000	0.24
1962	623,013	1,174,000,000	1,116,000	0.10
1963	452,910	623,000,000	682,000	0.11
1964	537,863	845,000,000	2,354,000	>0.28
1965	386,096	724,000,000	2,455,000	>0.34
			Average	0.25

[1] Including estimates for the Karluk River spawners below the weir.

0.10% to 0.40% (average, 0.25%) for fish spawned between 1958 and 1965 (Table 4-19). The figure listed for brood year 1964 (0.28%) would have been slightly higher had an estimate of the 5-year migrants been made in 1969. Additionally, the figure for brood year 1965 (0.34%) would have been considerably higher had the 4- and 5-year migrants been enumerated in 1969 and 1970. Although 5-year smolts were rare, 4-year smolts were second in abundance in most years. Unfortunately, the weir washed out in 1969 and smolt estimates were not made for many years thereafter. Barnaby (1944) calculated that egg to smolt survival for Karluk sockeye ranged from 0.45% to 0.90% depending on whether a 2:1 or a 4:1 ratio of return to escapement was assumed. The egg to smolt survival rates for the 1958–65 brood years (Table 4-19) were probably more realistic than those calculated by Barnaby (1944) because the former were not based on any assumptions except those that applied to the estimation of egg and smolt abundances, whereas the latter were based on hypothetical ratios of return to escapement and an unreasonably high average fecundity of 3,700 eggs (see Gard et al., 1987, Table 2). In a summary of eight other sockeye river systems, Foerster (1968:313–324) reported freshwater survival rates averaging 2.3%. Freshwater survival of Karluk sockeye averaging 0.25% was less than that in many other sockeye systems, one reason being that Karluk juveniles remained in the lake for a longer period of time.

Near Shore Sea Life

Few observations have been recorded of the early sea life of Karluk sockeye juveniles in the near shore and estuarine environments. The information presented here was obtained incidentally from beach seining for adults in the ocean off Karluk Spit or within Karluk Lagoon (Chamberlain, 1907). Although large-mesh seines were used, some juveniles were usually caught in each haul. On 8 June 1903, 67 young sockeye averaging 181 mm in length (range, 123–207 mm) were measured. An examination of 20 stomachs revealed that the sockeye were feeding mainly on small crustaceans, but not on fry of any species. In a similar manner, 30 young sockeye composed of 12 males averaging 136 mm (122–156 mm) and 18 females averaging 139 mm (125–164 mm) were collected on 3 July. Most of these had been feeding on small crustaceans, some contained pteropods, and two had some small blennies and sticklebacks. Small sockeye were present in the cannery seines outside the spit throughout the canning season, but none of the larger individuals observed in June were collected after 3 July. One haul within the lagoon on 24 July captured many young sockeye 30–145 mm in length and Chamberlain surmised that the smaller fish were from the hatchery and the larger fish were smolts from the lake. All were feeding on crustaceans and insects. Masses of intestinal worms were present in many of the fish.

A summary of smolt information follows: 1) Karluk smolts migrated to sea after 1–5 years in the lake. A 5-year residence in fresh water was unique and may be the longest known. 2) Timing of the smolt migration was fairly consistent from year to year. Smolts arrived at the outlet between 15 May and 26 May (average date 20 May) which was about six days earlier than they arrived at the lagoon. 3) Larger (and often older) smolts tended to migrate earlier than smaller smolts. 4) Estimated numbers of smolts migrating from the lake varied from 821,000 in 1982 to 4,700,000 in 1991. The large outmigration in 1991 may have been the result of lake fertilization in prior years. 5) Karluk smolts have become progressively shorter over the years. Much of this decrease came between 1903 and the 1925–36 period when they lost 34–37 mm in length. 6) The main food of young sockeye in the lake and at the river mouth was small crustaceans.

Life in the Ocean

Distribution and Migration in Offshore Waters

After leaving the Karluk River and adjacent shores, the majority of the juveniles moved to offshore feeding areas where they remained for 1–4 years before returning to spawn. The exact timing of the offshore migration was questionable, but Hartt and Dell (1986) presented a time series of maps showing that catches of juvenile sockeye off

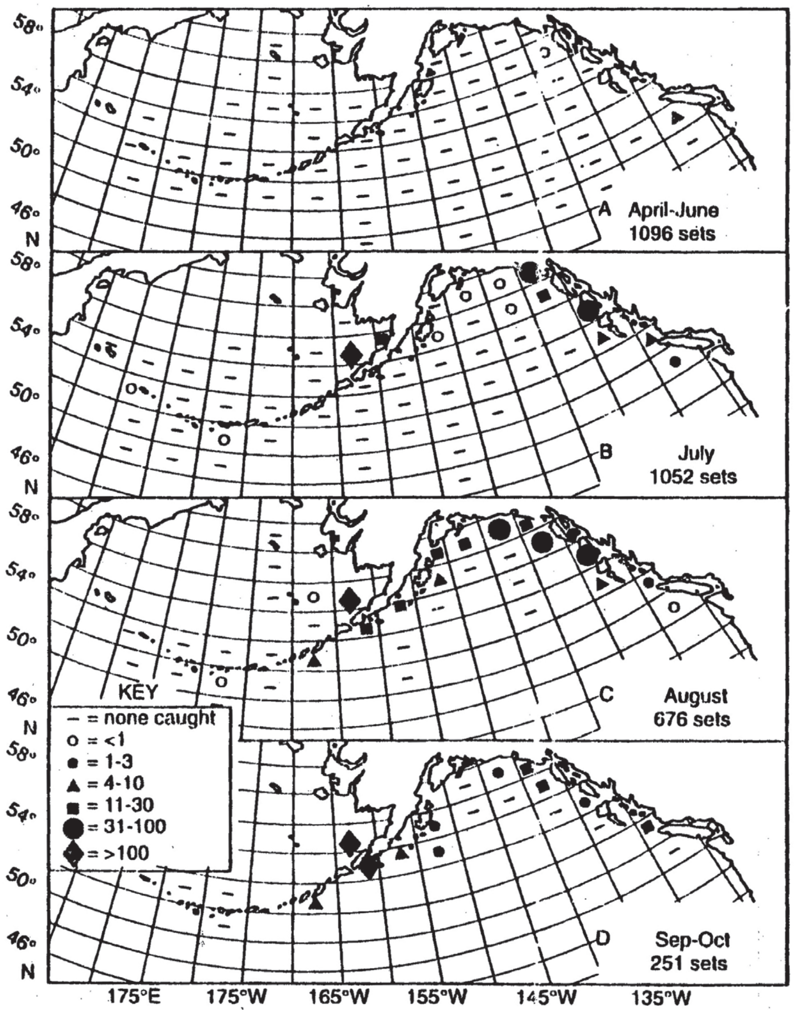


Figure 4-14. Mean catch per seine set of juvenile sockeye salmon by area and by time period; 3075 sets, 1956–70 (from Hartt and Dell, 1986, Fig. 3).

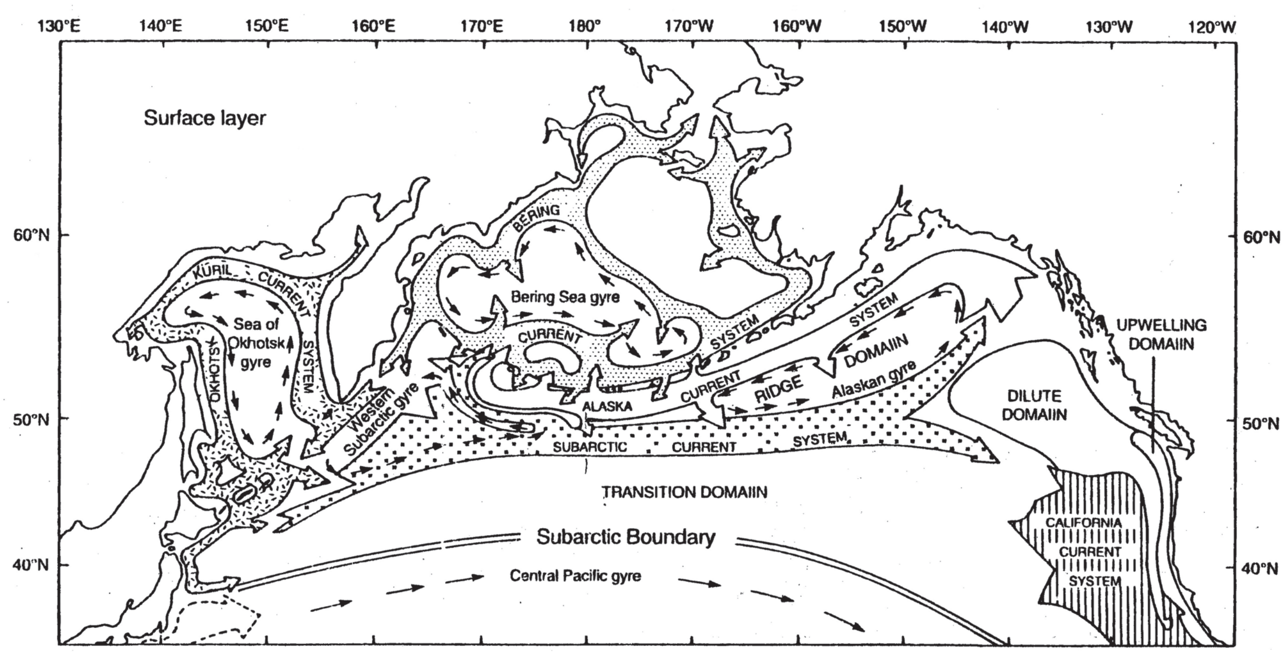


Figure 4-15. Schematic diagram indicating extent of surface layer domains and current systems in the Subarctic Pacific Region (from Favorite et al., 1976, Fig. 41).

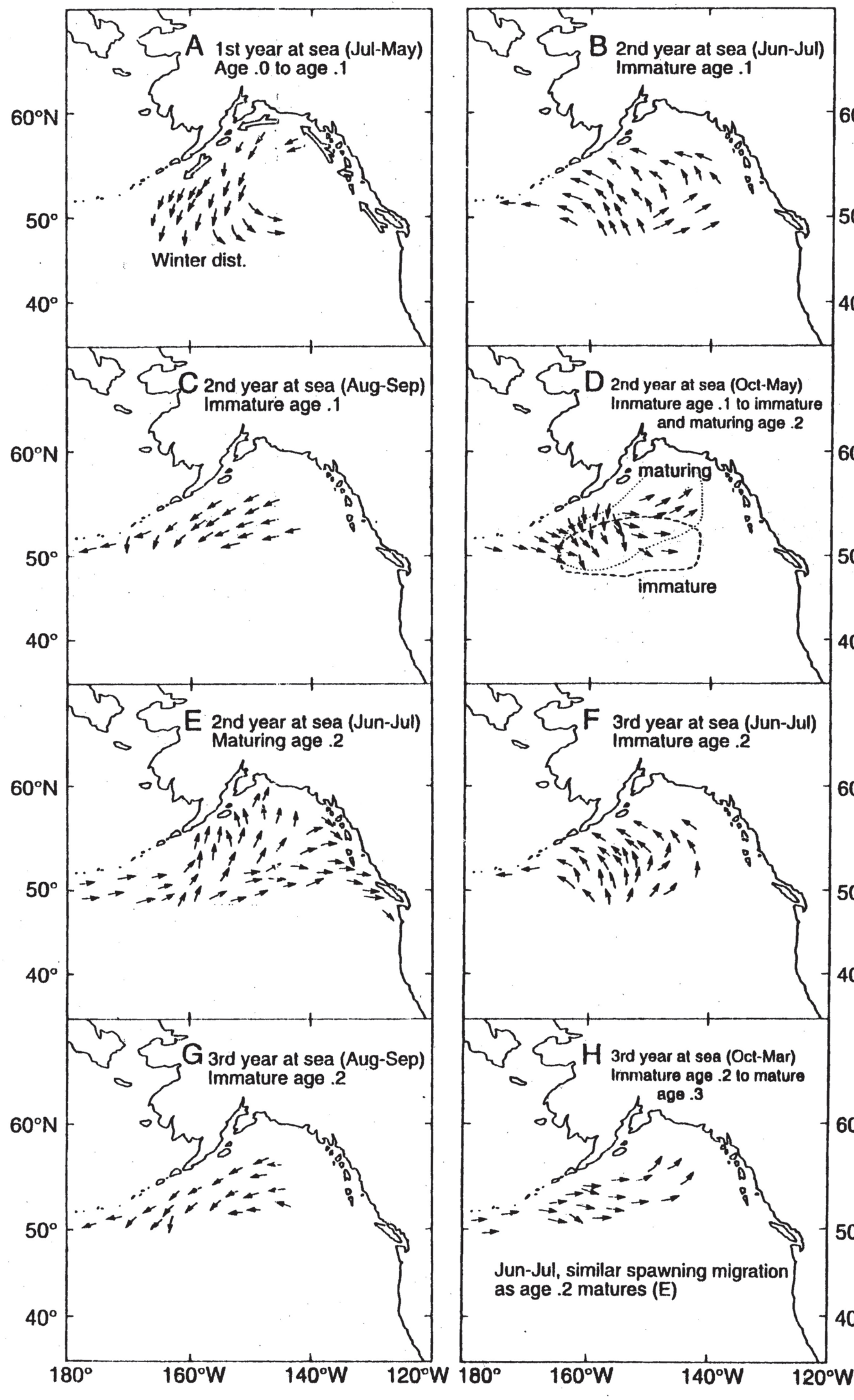


Figure 4-16. Model of migration of northeastern Pacific sockeye salmon (from French et al., 1976, Fig. 94).

Kodiak Island were largest between August and October (Fig. 4-14). Many of the sockeye in those catches were from northeastern Pacific rivers to the east or south of Kodiak Island, but some were surely from the Karluk River. The series of maps showed a northwest movement of eastern Pacific stocks followed by a southwestern movement during which the Karluk juveniles joined the others.

Several circular current systems known as gyres (Fig. 4-15) occur in the North Pacific Ocean and adjacent seas, and these gyres are often bounded by large masses of relatively stable water known as domains (Favorite et al., 1976). On the northern border of the Alaska gyre is the Alaska Current System into which the eastern Pacific sockeye stocks swim during their northwestern migration. This

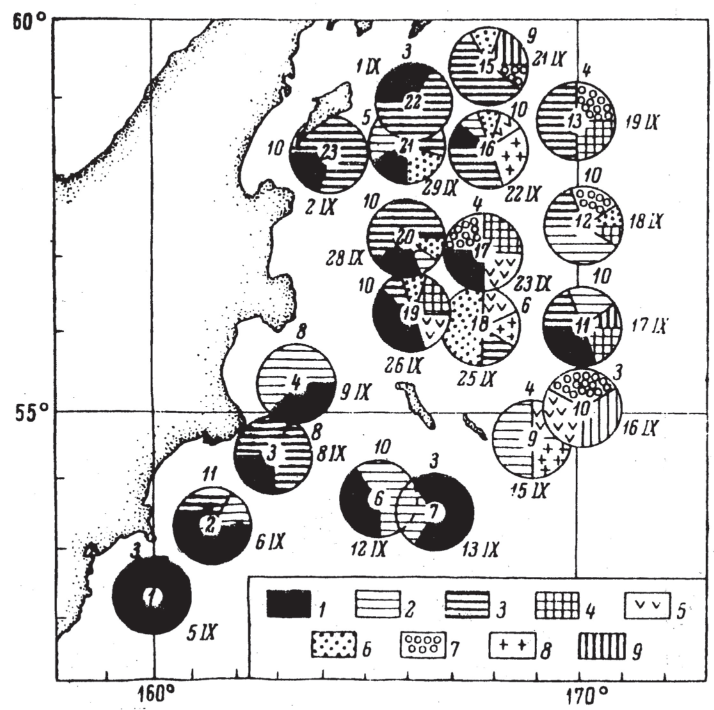


Figure 4-17. Distribution of local populations of sockeye salmon in the Commander Islands area of the Pacific Ocean and of the Bering Sea in September–October 1966 (from Konovalov, 1975, Fig. 104). (Key: 1 = population of Lake Kurilskoe; 2 = population of the Kamchatka River; 3 = undetermined populations of the NW coast of Kamchatka Peninsula; 4 = population of Lake Karluk; 5 = population of the Naknek River; 6 = population of the Wood River; 7 = population of the Egegik River; 8 = population of the Ugashik River; 9 = undetermined populations of Bristol Bay.)

system assists these stocks as well as the Karluk juveniles during their southwestern journeys and beyond.

French et al. (1976) described a generalized, circuitous migration of the northeastern Pacific stocks associated with the Alaska gyre (Fig. 4-16). A tagging experiment (Neave, 1964) suggested that some Karluk fish joined the northeastern Pacific stocks in this repetitious journey. Any mature 1-ocean Karluk fish (mainly age groups 4_3 and 5_4) returned to the natal river after one complete circle of the gyre (Fig. 4-16, Map B). Most Karluk fish, however, remained in the gyre a second year and returned to their spawning grounds principally as age groups 5_3 and 6_4 (Map E). Still other maturing Karluk fish (age groups 6_3 and 7_4) remained a third year in the gyre (Map H), and a few 4-ocean individuals repeated the process once again.

As is often the case with biological systems, the process described above was an oversimplification. Using presence of diagnostic parasites and scale characteristics to identify natal rivers, Konovalov (1975) found that Karluk sockeye seined in spring and early summer of 1963–66 occurred from 48–50°N and from 172°E to 172°W. That placed them somewhat south of the Aleutian chain and straddling the 180° meridian (Fig. 4-14). However, when seining was done in September and October 1966 east of Kamchatka, he found relatively large numbers of immature Karluk sockeye from 55°N to nearly 59°N and from 166–170°E (Fig. 4-17; Table 4-20). These fish, located well into the Bering Sea and only about 150 km off Kamchatka, were about 2,200 km from their natal river as measured along the most direct route—considerably farther than had previously been reported. They were accompanied by sockeye from Kamchatka and Bristol Bay. Commenting on that discovery, Konovalov (1975:236) stated: "In view of the relatively large number of fish (9 specimens) of this population caught, we may consider the feeding areas of sockeye of Lake Karluk as having shifted in relation to their spawning body of water on Kodiak Island somewhat to the west." The migration path followed by Karluk sockeye from their natal river to Kamchatka and return was a mystery. However, a working hypothesis is that they could follow the Alaska Current System from the Karluk River to about the 180th meridian, then turn north through an Aleutian Island pass into the Bering Current System which they could follow to near Kamchatka (Fig. 4-15). On the return, they could ride the Bearing Sea Current to the southeast, turn south through an Aleutian Island pass, and swim to the Subarctic Current System which would transport them to their natal river.

In additional to currents, temperature and salinity characteristics of oceanic water masses may influence sockeye distribution and migration. A copious literature addressing these topics exists, but effects on Karluk sockeye are not specifically mentioned. Generalities that may be made are that sockeye prefer colder water than do other species of Pacific salmon, and that temperature definitely influences their distribution and migration whereas salinity rarely has such an ef-

Table 4-20
Number of specimens of immature sockeye salmon of some local populations of different complexes in the catches of the northwestern part of the Pacific Ocean in September-October 1966 (From Konovalov, 1975, Table 51).

Drift number	Coordinates		Kamchatkan complex				Bristol Bay complex					Pacifico-Alaskan complex
	N Latitude	E Longitude	Lake Kurilskoe	Lake Azabachie	Kamchatka River	Eastern Coast	Wood River	Naknek River	Egegik River	Ugashik River	Kvichak River	Lake Karluk
1	52°20′	160°00′	3	–	–	–	–	–	–	–	–	–
2	53°20′	161°20′	6	–	1	4	–	–	–	–	–	–
3	54°20′	162°46′	2	–	2	4	–	–	–	–	–	–
4	55°20′	163°23′	3	3	2	–	–	–	–	–	–	–
6	53°42′	165°20′	4	5	1	–	–	–	–	–	–	–
7	53°32′	166°40′	2	–	1	–	–	–	–	–	–	–
9	54°35′	168°58′	–	1	1	–	–	1	–	1	–	–
10	55°02′	170°10′	–	–	–	–	–	1	1	–	–	1
11	56°07′	170°07′	3	–	2	2	–	1	–	–	–	2
12	57°27′	170°10′	–	1	3	2	1	–	2	–	–	2
13	58°43′	170°10′	–	–	–	2	–	–	1	–	–	1
15	59°27′	167°54′	–	1	1	3	1	–	1	–	2	–
16	58°23′	167°52′	1	–	1	3	1	1	–	3	–	–
17	57°05′	167°50′	1	–	–	–	–	1	1	–	–	1
18	56°05′	167°48′	–	–	1	–	3	–	–	1	–	–
19	56°18′	166°10′	4	–	–	1	1	2	–	–	–	2
20	57°16′	166°00′	2	–	1	4	1	1	–	–	–	1
21	58°25′	166°00′	1	2	1	–	1	–	–	–	–	–
22	59°01′	166°10′	1	–	1	1	–	–	–	–	–	–
23	58°19′	164°10′	2	1	2	5	–	–	–	–	–	–

fect. Two or more physical factors may operate in concert, but no single environmental element wholly determines the distribution or migration of sockeye salmon. For a thorough discussion of these topics see Burgner (1991:70–83).

Vertical Distribution

A few studies have been conducted on vertical distribution of salmon at sea. Manzer (1964) reported that sockeye were caught down to a depth of 61 m in the Gulf of Alaska, but most were caught in the upper levels. He also found that they tended to be caught closer to the surface at night. During an investigation in the northwestern Pacific Ocean and Bering Sea, Machidori (1966) reported that immature and maturing sockeye were mostly in the upper 10 m and that they were somewhat shallower at night. The efficient Japanese high-seas gill net fishery set gear down to a depth of only 8 m (Fukuhara, 1971) and their longline salmon fishery placed gear a scant 1–2 m below the surface. Finally, French et al. (1976) reported that 90% of the sockeye caught in vertical gill nets in the northeastern Pacific Ocean were in the top 15 m and that none were caught below 30 m. After reviewing these observations, Burgner (1991) concluded that salmon generally occurred in near-surface waters. Because two of the investigators reported that sockeye were caught closer to the surface at night, a diel vertical migration may have occurred. Pella (1968) presented conclusive evidence of a diel vertical migration in juvenile sockeye in Lake Aleknagik. It would seem likely that planktivorous fish such as sockeye salmon would have a diel vertical migration pattern in both fresh and salt water because plankton has long been known to exhibit such movements.

Rates of Travel

Rates of travel of sockeye at sea vary greatly with stage of maturity, distance to be covered, and season. They are usually determined by tagging fish at a certain location and noting how long it takes them to reach a second location. For example, maturing sockeye traveled along the north coast of Kodiak Island from Uganik Bay to Karluk River at a mean rate of 8 km/day (Rich and Morton, 1930) whereas maturing salmon traveled from the Aleutian Islands to Bristol Bay at an average rate of 43 km/day (Hartt, 1966). The Bristol Bay fish had to travel a much longer distance. Hartt (1966) also reported that the rate

of travel of maturing Bristol Bay sockeye increased as the season progressed and that immature fish moved more slowly than maturing individuals. Gard (1973) also found that the rate of travel of maturing sockeye migrating up the upper Karluk River increased from 2 km/day to 6 km/day between 1 August and 1 October.

Migration Mechanisms

One of the great mysteries of the biological world is how salmon navigate on the high seas and find their way back to their natal streams. A number of hypotheses have been proposed to explain this phenomenon, but the most likely explanation is the salmon's perception of celestial and magnetic cues, accompanied by their ability to translate this information into a workable navigational system. Several studies have demonstrated that sockeye fry and smolts utilize celestial and magnetic cues during their migrations in lakes (Groot, 1965; Brannon, 1972; Quinn, 1980; Quinn and Brannon, 1982). However, that sockeye use celestial and magnetic cues to navigate in the open ocean where the distances traveled may be 3,000–4,000 km has not been documented. To navigate in this manner, the sockeye would have to know the time of season and day and approximately where they are and where they are to go. With these considerations in mind, Quinn (1982b) proposed that salmon navigate at sea using a map based on inclination and declination of the earth's magnetic field, a celestial and magnetic compass, and a calendar which is in effect a seasonal clock. Day length is the most likely environmental factor that drives the clock.

If Quinn's model is correct, there is a close similarity between the methods used by sockeye and humans (prior to satellite navigation) to navigate on the high seas: Sockeye would have a map; humans have a nautical chart. Sockeye would have an internal magnetic compass which gives them horizontal and vertical information; humans have an external magnetic compass which gives them a horizontal course. Sockeye would have a biological clock; humans have a chronometer; sockeye would estimate the elevation of the sun by eye; humans use a sextant to do the same. Finally, sockeye would integrate within their brains the information they perceive to give them a geographical position; humans use a nautical almanac, a sight reduction table, and a position plotting sheet for that purpose.

Near the end of their return home, the sockeye switch from their high seas navigational system to a near shore olfactory system as they can smell their natal river. This ability was imprinted upon them before they migrated to sea as smolts (Hasler et al., 1978).

Food and Growth

In contrast to the paucity of food habit studies for juvenile sockeye in Karluk Lake, considerable feeding information has been acquired in the northeastern Pacific Ocean and the Bering Sea for sockeye of various stocks. In a summary of stomach analysis information from many areas presented by Foerster (1968) and French et al. (1976), Burgner (1991) stated: "Euphausiids, hyperiid amphipods, small fish, and squid were the groups most frequently listed as main food items, with copepods, pteropods, and crustacean larvae listed as of lesser importance. The fish included lantern fish (Myctophidae) and juvenile cod (Gadidae) in the central North Pacific Ocean. In the eastern Bering Sea, juvenile sockeye (aged-0) fed on larval capelin (*Mallotus villosus*), sand lance (*Ammodytes hexapterus*), and herring (*Clupea harengus pallasi*)."

The northeastern Pacific Ocean, including the Alaska Current and Ridge systems, is known to be a favored Karluk sockeye feeding area (Fig. 4-15). In the eastern Alaska Current, Le Brasseur (1966) found that fish followed by euphausiids were the most important foods in mature sockeye stomachs, whereas the immature sockeye stomachs contained amphipods and euphausiids in equal amounts. Although no stomachs were examined, McAlister et al. (1969) reported immature sockeye concentrated in autumn in the Ridge Domain where there was an abundance of euphausiids. Because the areas sampled by Le Brassure and McAlister et al. are adjacent and high concentrations of euphausiids were found in the stomachs and in the environment, feeding was probably associated more with availability than with preferences for specific organisms.

The western Bering Sea off Kamchatka is another known feeding area for Karluk sockeye. Andrievskaya (1957) found that sockeye stomachs from this area contained 60% euphausiids, 28% young fish, and 13% copepods, plus some young squids, crab larvae, pteropods, and insects. He also examined sockeye stomachs from just south of the western Aleutian Islands and reported that copepods were dominant (53%) followed by euphausiids, amphipods, pteropods and young fish in equal proportions.

Some contradictory and unusual discoveries were reported by investigators of sockeye food habits. Both Le Brasseur (1966) and Dell (1963) reported differences in food preferences by maturity stages of sockeye with euphausiids being more favored by immatures. However, Ito (1964) and Andrievskaya (1957) found no food preference by maturity stage. Additionally, Andrievskaya reported that sockeye contained a significantly less volume

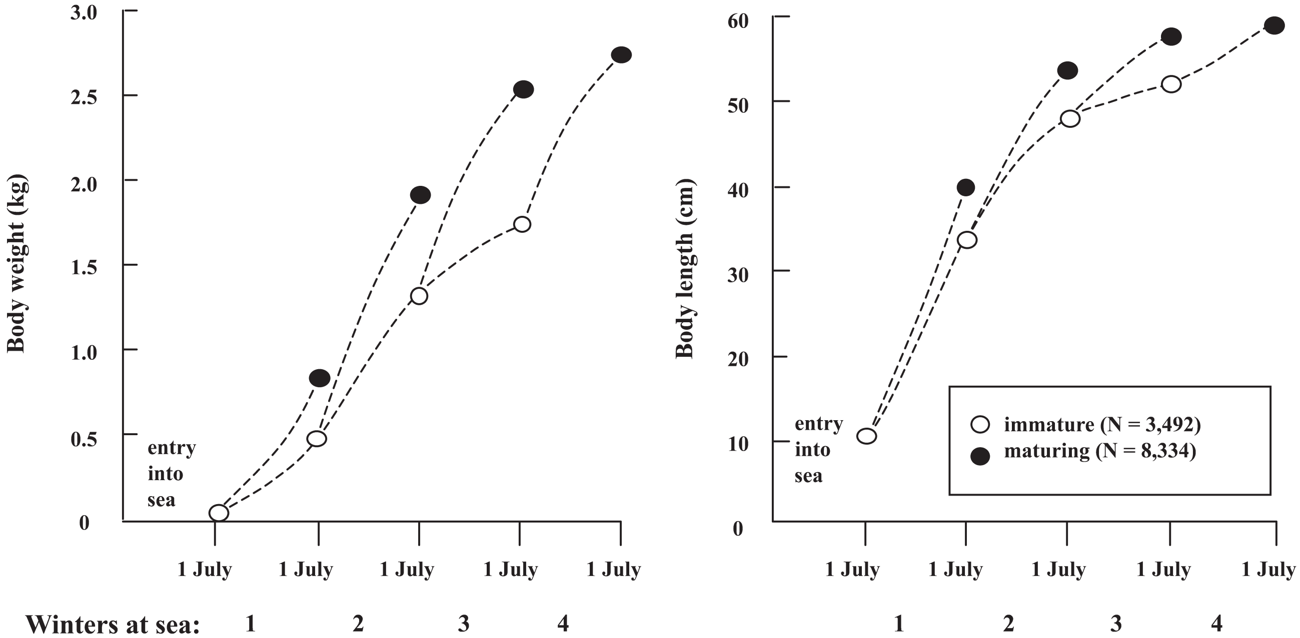


Figure 4-18. Estimated mean body weights and lengths of sockeye salmon on 1 July (Lander et al., 1966, in French et al., 1976, Fig. 36). Connecting lines indicate related stages, not actual growth.

of food than did pink or chum salmon even though their diets were similar. Perhaps pink and chum gorge themselves more than sockeye do because the former generally spend less time feeding before they spawn.

Size and Growth at Sea

There is little specific information on size and growth at sea for Karluk sockeye, but there is some general information for combined stocks (Fig. 4-18). Growth in length is greatest during the first year at sea and decreases progressively each year thereafter, whereas growth in weight is greatest in the second year followed by sequential decreases. At a given age, maturing fish are larger than immature fish. Also, male sockeye are larger than females by the spring of their second winter at sea and remain longer until death (Lander and Tanonaka, 1964).

It was formerly thought that little sockeye growth occurs in winter and early spring, but French et al. (1976) present average lengths of combined stocks from the North Pacific and Bering Sea which shows that growth continues through most of the year (Fig. 4-19). Appreciable growth occurred between September and winter and between winter and April.

Indirect evidence of seasonal trends in growth of Karluk sockeye in the sea comes from scales. The most common Karluk age group is the 5_3 which indicates that the fish spent 3 years in freshwater and 2 years in the ocean (Fig. 4-20). Moving out from the center (focus) of the scale we see the first two annuli, the area where the circuli are close together, which occurred in freshwater. These two annuli formed during the winter in the lake. After annulus 2 the fish went to sea and the circuli are wide apart and numerous, indicating a long period of fast growth. During the first winter at sea annulus 3 was formed and was followed by a second period of strong growth terminated by annulus 4, after which there was some spring growth before the fish returned to the natal river. Bilton and Ludwig (1966), after examining sockeye scales from the Gulf of Alaska collected in January and February, concluded that the annual ring was probably formed between November and January and, on the average, was completed in January. Therefore, if body growth slowed down during the formation of the annual ring, the slow growth was for a relatively short period of time.

Survival in the Ocean

Total ocean survival of Karluk sockeye has been determined by marking smolts and recording the presence of marked adults in future runs and by estimating the number of migrating smolts and determining the number of returning brood year adults. For both methods, numbers of fish in the catch and escapement had to be determined, as well as appropriate age structures. See Barnaby (1944) and Gard and Drucker (1966a, b) for further details. These ocean survival rates included some time in freshwater because the weirs where enumeration or marking were conducted were 6–37 km from the sea.

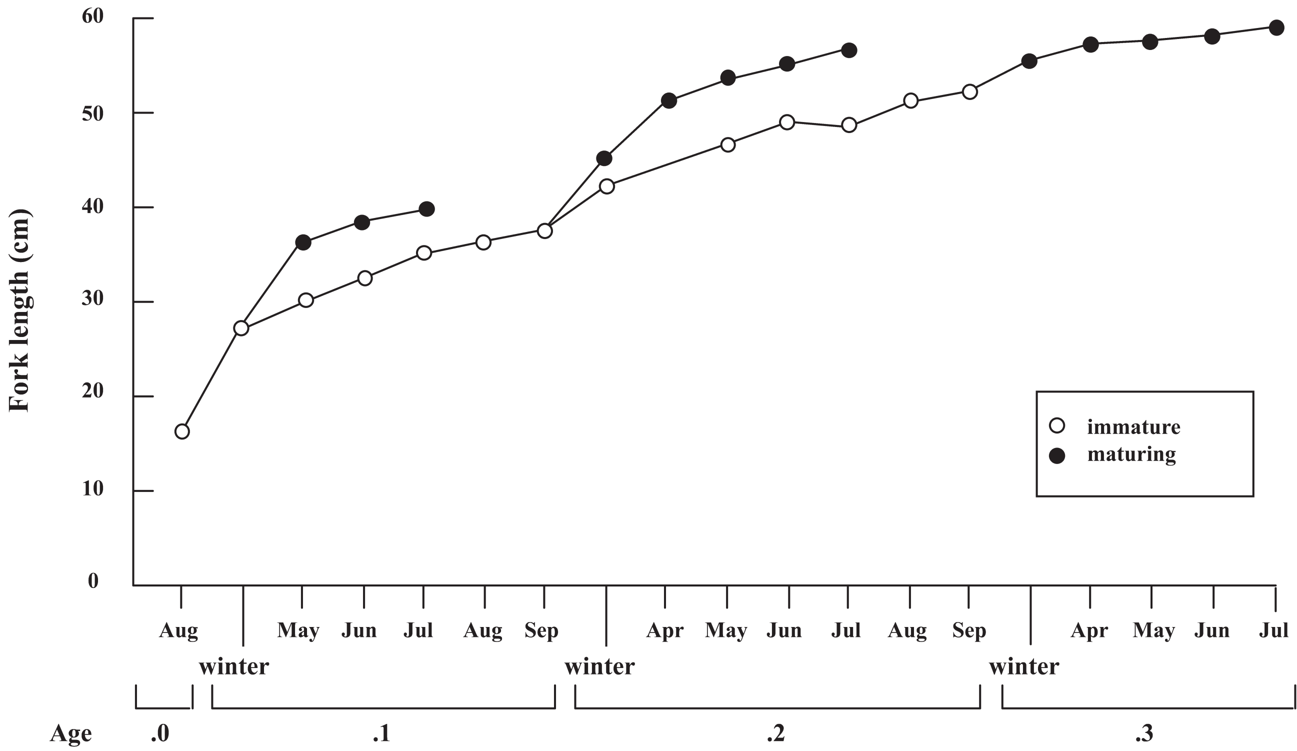


Figure 4-19. Average fork lengths of sockeye salmon taken at sea by ocean age and time periods (from French et al., 1976, Fig. 40). Data from gillnet catches, combined sexes, and for all areas in the North Pacific Ocean and Bering Sea.

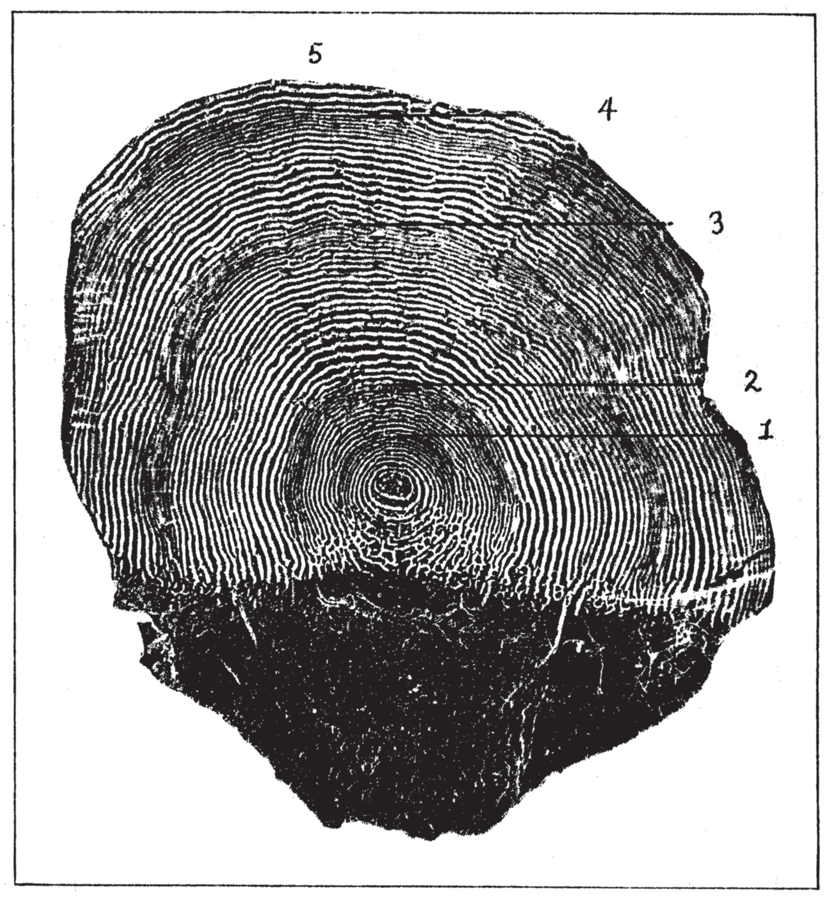


Figure 4-20. Scale from an age 5_3 male sockeye salmon taken on 9 June 1924 at the lower Karluk River weir (from Gilbert and Rich, 1927).

Table 4-21
Marine survival of sockeye salmon from Karluk Lake (from Drucker, 1970).

Smolt migration year	Number of smolts (1,000s)	Returning adults (1000s) by year								Survival (%)
		1962	1963	1964	1965	1966	1967	1968	Total	
1961	1694	28.1	418.0	82.6	0.4				529.1	31.2
1962	1444		17.6	631.6	66.1	0.7			716.0	49.6
1963	1540			36.8	469.5	71.1			577.4	37.5
1964	1561				14.0	656.5	129.5	0.3	800.3	51.3
1965	1469					6.8	408.1	78.9	>493.8	>33.6
1966	1082						5.4	379.0	>384.4	>35.5
									Average	>39.8

The first ocean survival rates for Karluk sockeye were determined by Barnaby (1944). He marked migrating smolts at the Lagoon weir by removing the adipose fin and one or both of the ventral fins and recovering the marked returning adults from canneries on Karluk Spit and at Larsen and Uyak bays. Ocean survival rates so determined for smolt migration years 1926 and 1929 through 1933 were 20.8% (incomplete), 22.3%, 21.0%, 23.6%, 20.5%, and 20.5%, respectively, with a 6-year mean of 21.4%. These survival rates were unusually uniform and high when compared to a 6–17% variation for five years of data from Chilko Lake or a 2–18% variation for 18 years of data from Cultus Lake (Ricker, 1962, Fig. 1).

When Barnaby combined all his data into 3-freshwater and 4-freshwater groups, he found that respective ocean survival rates were 17.4% and 25.7%. That would suggest that older (and also longer) smolts survived better in the ocean than did younger (and shorter) smolts. However, any survival advantage enjoyed by the older fish in the ocean could have been offset by increased freshwater mortality that resulted from spending an additional year in the lake. In an evaluation of six sockeye populations from North America and Siberia, Ricker (1962, Fig. 1) also demonstrated that ocean survival rate generally increased in larger smolts.

Although Barnaby recognized that there may have been differential mortality between marked and unmarked fish, he did not correct his survival rates accordingly because he did not believe the differences would be very great and because marked fish held in tanks for several days did not display ill effects. However, Ricker (1962) believed that delayed mortality due to marking may have occurred and corrected Barnaby's survival rates using information obtained at Cultus Lake by Foerster (1934, 1936, 1937). These corrections resulted in increased ocean survival of 3-freshwater Karluk fish from 17.4% to 27.4% and of 4-freshwater fish from 25.7% to 34.2%.

Recent ocean survival rates of sockeye (1962–83) for nine Alaskan lakes including Karluk combined with those from Ricker (1962, Fig. 1) indicated that a polynomial curve described the relationship between smolt length and marine survival better ($P < 0.001$, F-test) than a straight line (not significant) (Koenings and Burkett, 1987a, Fig. 8). Marine survival increased with increasing smolt length to about 110 mm, leveled off, and then decreased after a length of about 130 mm. Also, ocean survival rates of many sockeye populations have increased on the average during the past 30–50 years. This was especially evident for Karluk Lake where sockeye marine survival rates between 1961 and 1966 ranged from 31.2% to 51.3% (Table 4-21) and in later years up to about 60% (Koenings and Burkett, 1987a).

Harvest

Sockeye salmon have been harvested in the Karluk River for over 200 years. In 1785–86 a party of Russians, Aleuts, and Alutiiq established a post on the Karluk River and harvested salmon from the river to produce dried and salted fish for native fur hunting parties and for local use. These activities continued sporadically until the United States purchased Alaska from the Russians and three salting operations were founded in 1867. Three years later, the Alaska Fur Trading Company and Alaska Commercial Company entered the sockeye salting business which increased in succeeding years. Karluk River was becoming an important sockeye salmon processing center and Bean (1887) stated: "Karluk River, on the west side of Kodiak Island, furnishes more salt salmon than any other Alaska stream, about sixteen hundred barrels having been secured there during the season of 1880 by two firms." Addi-

tionally, Captain Bowen told Bean that at least 100,000 salmon were caught and dried.

Commercial fishing at Karluk is often considered to have started in 1882 when the first cannery was constructed on Karluk Spit by Oliver Smith and Charles Hirsch; it was subsequently known as the Karluk Packing Company in 1884. This cannery was followed by two others constructed on Karluk Spit, another just west of the Karluk River mouth, and a fourth at Larsen Bay in 1888. Still another cannery was built on the Spit in 1889, bringing the total to five canneries (Gilbert and Rich, 1927, Table 1). The result of this rapid expansion of processing capacity was over production of canned salmon in 1888–89.

There were many restrictions relating to permissible fishing gear and areas open to fishing. All salmon fishing was conducted within Karluk Lagoon and River through 1888, but in 1889 beach seining in ocean water outside the river mouth was begun. Karluk River and Lagoon were closed to commercial fishing in 1918. Gill nets, purse seines, and stationary and floating traps were all used at various times in the commercial Karluk salmon fishery; restrictions came and were sometimes rescinded later. Purse seines and floating traps were prohibited in 1924, with the seines being legalized in 1933. However, in 1946 seines were disallowed within 500 yards of the Karluk River mouth. Fish traps were prohibited in the Kodiak Region for commercial fishing in 1958 and after statehood were ruled illegal for virtually all of Alaska in 1960.

Sockeye salmon catches for the Karluk River have varied enormously since the inception of the fishery in 1882, from a high of nearly 4 million in 1901 to lows of only a few thousand in 1955 and 1971–73 when the fishery was closed due to low escapements, and again in 1989 when the *Exxon Valdez* oil spill occurred (Fig. 1-2). Let us examine the changes in catch that occurred by mostly 10-year periods (Table 4-22). From 1882 to 1890 the fishery grew rapidly from about 60,000 to over 3 million fish (average 1.3 million). During 1891–1900 the fishery reached its zenith with a mean catch of 2.5 million and this was followed by another decade with large harvests that averaged 2.2 million fish. Thereafter, the numbers decreased progressively despite a huge catch of 2.4 million in 1926. It appeared that the fishery bottomed out during the 1950s because a modest increase occurred in the 1960s (average, 226,000), but the 1970s were a disaster with a mean of only 120,000 taken. During the 1980s numbers improved somewhat, but the average catch doubled to 575,000 in the 1990s and 555,000 in the 2001–10 period. Various theories that attempt to explain the decline and recovery of the catch (and run) are discussed in Chapter 11.

Table 4-22
Average catch of Karluk River sockeye salmon by 10-year periods. (See Fig. 1-2 for data sources.)

Years	Average catch
1882–1890	1,332,277
1891–1900	2,503,987
1901–1910	2,205,012
1911–1920	1,342,631
1921–1930	974,198
1931–1940	799,054
1941–1950	487,353
1951–1960	144,710
1961–1970	226,164
1971–1980	120,131
1981–1990	273,916
1991–2000	575,025
2001–2010	555,420

Cyclic fluctuations in abundance of sockeye occurred in a number of rivers and were apparent in catches from Karluk during the earlier years of the fishery. Excluding the earliest years through 1895 when the fishery was building up to consistently high catches, 5-year cycles began to appear (Fig. 1-2). The 1896 catch was high and was followed by a somewhat lower catch in 1897, a low catch in 1898, a still lower catch in 1899, and a high catch again in 1900. This pattern with minor variations repeated itself during four successive cycles, but it started to weaken with the 1921 cycle when the catch in the second year was the lowest of the five (Gilbert and Rich, 1927, Fig. 7). Thereafter, the 5-year cycles disappeared and never returned. It was reasonable to expect that a 5-year cycle would develop at Karluk because the majority of the fish mature at five years of age, i.e. if catch and escapement are generally proportional, a high catch one year should be followed by a high catch five years hence. The mechanism involved in maintaining cycles could be cannibalism by a large year class on subsequent year classes or interactions between the spring and fall runs. Karluk Lake, with up to five year classes of juveniles present at any one time, would be a likely situation where cannibalism could be involved. Other possibilities for interaction between year classes could be depletion of their food supply by the dominant year class, or depletion of oxygen in the spawning gravels, caused by abundant decomposing eggs deposited by the dominant year class, thus lowering survival of

subsequent year classes (Ricker and Smith, 1975). Obviously, some changes occurred within Karluk Lake that caused the cycles to disappear and may also be responsible for the depletion of the runs.

Conclusion

Much has been learned during the past years of study about the life history of the unique and diverse Karluk sockeye salmon. However, there is one important aspect about which we know virtually nothing. This is the food habits of the rapidly-growing pre-smolts in the lake during the late fall and winter and the potential food then available. The proportion of marine nitrogen isotopes present in pre-smolts increased sharply at that time and this change was possibly from cannibalism on younger sockeye or predation on sticklebacks (Kline, 1993; Kline and Goering, 1993). Only a fall and winter food habits study will verify or disprove this hypothesis.

CHAPTER 5

Are Karluk River Sockeye Salmon Differentiated into Subpopulations?

It's one interbreeding population and Darwin be damned!

Citing the existence of distinct spring and fall sockeye salmon runs in the Karluk system,[1] most early investigators suspected there must have been two or more self-sustaining units whose differences were heritable.[2] However, in 1958 George Rounsefell startled the fishery science community when he declared that the entire Karluk River sockeye salmon run was composed of only one interbreeding population (equivalent to the subpopulation of Marr (1957)). This declaration proved to be a clarion call for many subsequent investigators who believed subpopulations existed in the system. It was important that the matter be resolved because effective management and one of the theories of the decline of Karluk sockeye were based on the existence of subpopulations. A summary of observations, thoughts, and research relevant to the subpopulation question follows.

Prior to 1958: The Early Era

During the early years of the Karluk River sockeye salmon investigations, the theory of evolution was already widely accepted by biologists. Every biologist had heard of Charles Darwin and most of them knew that one of the conditions required for the evolution of genetically distinct entities (subpopulations) was reproductive isolation. Another concept that was gaining acceptance around the turn of the century was the home stream theory. This was the belief that when a salmon returned to freshwater to spawn it sought the stream in which it was hatched. If homing occurred to two different spawning areas or to one spawning area at two different times, reproductive isolation would follow and the stage would be set for the evolution of subpopulations.

[1] A thorough treatment of Seasonal Run Distribution is given in Chapter 6.

[2] Such units were commonly called "races," but Marr (1957) preferred the term "subpopulations" which is used in this report.

Isolation by Spawning Area

First, let us consider observations where sockeye salmon migrated to two separate streams to spawn. Moser (1899) noted the large difference in size as well as smaller differences in form, color, and texture of sockeye salmon in different streams, and stated that "Upon this hangs the idea persisted in by many fishermen, that salmon do return to their parent stream; and if the differences mentioned do exist, the theory based on them must have great weight." Rutter (1903a) discussed the home stream idea:

> There is a widespread belief that when a salmon returns to breed it seeks the stream in which it was hatched, though there is very little evidence that such is true. . . . The employees of the Alaska Packers' Association state that the red salmon taken at Uganuk are always smaller than those taken at Karluk. . . . This seems to indicate that the salmon of two localities are distinct, but the larger salmon may go to Karluk, not because they have been hatched in Karluk Lake, but because they are larger.

Gilbert and Rich (1927) apparently believed in the existence of subpopulations because they stated that ". . . each of these species [of Pacific salmon] has an independent, self-perpetuating colony in each of the streams that it inhabits. Each colony forms a self-contained unit, the members of which consistently interbreed, their progeny returning to their native stream at sexual maturity." This anecdotal information does not prove the existence of homing or of subpopulations, but it suggests that both might occur.

To determine if subpopulations existed in different spawning areas, DeLacy and Morton obtained morphometric data (measurements of body proportions), meristic data (numbers of gill rakers, eggs, and vertebrae), and freshwater age data from otoliths and scales of over 1,000 salmon collected from various spawning grounds in Karluk Lake and its tributaries during 1941 and 1942. Additionally, large numbers of fish were

tagged at the weir, and their appearance on the spawning grounds was documented. When statistical comparisons were made, several significant "t" values were found in the data (probably gill raker and vertebral counts) from Canyon Creek and O'Malley River.[3] Also, no significant differences were discovered between either vertebral or gill raker counts from samples collected in 1941 as compared to samples collected in 1942 at the same time and place.[4] Further, the freshwater age analysis revealed statistically significant differences between the proportions of 3- and 4-year freshwater fish comprising certain samples.[5]

These results support the theory that Karluk River sockeye salmon home to the same tributary in which they originate and add evidence of the existence of different subpopulations in different tributaries of the lake. Such information is more convincing than anecdotal information. However, we now know that part of each character difference observed may have been the result of environmental as well as hereditary influences.

Isolation by Time

Much of the interest in the subpopulation question at the Karluk River system was focused on the early and late runs. There were hints of the existence of the bimodal nature of the run during the period of Russian occupation (1741–1867), but the first well-documented statement was that by the ichthyologist Tarleton H. Bean (1887) when he referred to the 1880 salmon runs at the Karluk River:

> [Speaking of the Karluk River salmon in 1880] In the beginning of July red salmon became scarce, and after the run of humpbacks (*O. gorbuscha*) set in (July 12), the red salmon (*O. nerka*) disappeared altogether. Smith & Hirsch stopped fishing until August 14, when the red salmon again made their appearance.

In 1900, Fassett (1902) was the first to refer to the early and late runs as the spring and fall runs. He said that eggs of spring-run spawners seemed more vigorous and hatched more rapidly than those of fall-run spawners, but both were of better quality than eggs of midseason spawners. He summarized that "It is also apparent that in considering the hatching of redfish at Karluk the two runs must be treated separately—the runs are so marked and the prevailing conditions so radically different." Fassett also pointed out that at Karluk fall-run fish were larger and had more and larger eggs than did spring-run fish.[6] Rich stated that the large pink salmon run of 1924 damaged only the red salmon that were spawning during the midseason, making it likely that the offspring tended to return and spawn at the same time as their parents.[7] This is evidence in support of the existence of both homing and subpopulations.

In his monumental 16-year (1921–36) study of Karluk River sockeye salmon, Barnaby (1944) discussed the existence of two runs:

> It appears that there are two distinct red salmon runs to the Karluk River each year, the spring run which reaches a maximum during June and the fall run which reaches a maximum between the last week of July and the first week of September.
>
> Whether or not the separation between the two groups has been sufficient to produce any anatomical differences that might be detected biometrically has not been determined conclusively. Even though differences between spring and fall runs could not be detected biometrically, such an absence of differences would not repudiate the theory of two populations of red salmon inhabiting one watershed and spawning in the same gravel.
>
> . . . it would seem that there are two self-perpetuating components of the red-salmon population in the watershed, and that each should be given adequate protection.

Despite the evidence cited above, there was still some doubt as to the existence of self-perpetuating spring and fall runs. Therefore, further studies by Allan DeLacy were conducted between 1939 and 1942 to clarify the matter.[8] During the first two years only morphometric data were taken from nearly 1,000 fish from Karluk Lagoon and the nearby ocean, but no consistent differences were found between spring- and fall-run fish. The studies were continued in 1941–42 when samples were collected at Karluk Lake as described in the previous section. Apparently, DeLacy found some evidence that spring and fall runs were self-perpetuating

[3] Letter (5 Nov. 1942) from Allan C. DeLacy, Assistant Aquatic Biologist, Alaska Fishery Investigations, Seattle, WA, to W. M. Morton, FWS, Stanford University, Palo Alto, CA. Located at NARA, Anchorage, AK. USBF October 1942 Monthly Report. Located at NARA, Anchorage, AK.

[4] USBF October 1942 Monthly Report. Located at NARA, Anchorage, AK.

[5] USBF November 1942 Monthly Report. Located at NARA, Anchorage, AK.

[6] Fassett, H. C. 1910. Report on the salmon hatchery operated by the Alaska Packers Association on Karluk Lagoon, Kadiak Island, Alaska. Unpubl. report. 25 p. Located at Alaska Historical Collections, Alaska State Library, Juneau.

[7] Extract of letter (4 Nov. 1929) from Dr. Rich to O'Malley, Department of Commerce, USBF. Located at NARA, Anchorage, AK.

[8] 1) USBF September 1940 Monthly Report, and
2) O'Brien, James. 1939 notebook. Both located at NARA, Anchorage, AK.

since he stated that "The data in at least one instance also indicate the existence of a significant difference between the spring and fall runs to a particular section of the Karluk drainage system."[9]

Since we were unable to locate a report for DeLacy's four years of subpopulation studies, we do not know (in most cases) which characters were diagnostic and which spawning grounds were sampled. The fragments of information we did locate in personal letters and in-house reports supported the existence of temporal as well as spatial subpopulations in the Karluk River sockeye salmon. In any event, this was pioneering work, and DeLacy was attempting to answer a very important question.

Perhaps because DeLacy did not produce a report of his subpopulation studies, Shuman initially was unconvinced that the spring and fall runs were separate and distinct. Shuman stated that "However, it has never been demonstrated that spring fish beget spring fish exclusively, or that fall fish beget fall fish exclusively, and until this is done it has been considered advisable to deal with the yearly run as a whole".[10] To investigate this matter further during 1945–48, Shuman and his assistant Nelson tagged thousands of sockeye salmon from all seasons of the run at the weir (located near Karluk Lake outlet after 1944). Tagged fish were noted on the spawning grounds during periodic stream surveys. Their study showed that spring-run fish were mostly stream spawners and fall-run fish were mostly lake spawners.[11] In addition to their tagging information, Shuman received a letter from Willis Rich on 16 August 1946 recommending that he treat the two Karluk runs separately "at least unless and until it can be proved that the two runs are *not* independent."[12] Apparently, the tagging information and Rich's letter convinced Shuman that "Evidence has been obtained which indicates that the spring and fall runs at Karluk are separate and distinct; they should be handled as such."[13]

In concert with Shuman's preceding statement, Thompson (1950) proposed a theory of the decline of the Karluk River sockeye salmon run, based on the existence of subpopulations. Also, during at least 1948–53, Bevan and Walker (Bevan, 1953) collected subpopulation data on Karluk River sockeye salmon. Regular counts of adult sockeye salmon were made on the spawning grounds and many thousands of length measurements and scales were obtained from adults in the fishery, at Karluk River weir, and at the spawning grounds. Their results showed that sockeye adults had distinct times and locations for spawning in the Karluk Lake habitats. They also found that freshwater growth of spring and fall runs at Canyon Creek was significantly different. Further, fall-run adults in the fishery were longer than spring-run adults; this difference prevailed at the Karluk River weir and on the Karluk Lake spawning grounds. With the exception noted, all of this information appeared only in unpublished reports or in data folders of graphs and tables.[14] Most likely, Bevan and Walker were searching for evidence of subpop-

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9 USBF December 1941 Monthly Report. Located at NARA, Anchorage, AK.

10 Shuman, Richard F. 1945. Observations on escapements and returns of red salmon at the Karluk River. FWS, Division of Fishery Biology. Unpubl. report. 17 p. Located at ABL files, Auke Bay, AK.

11 Letter (28 Feb. 1947) from RFS [Richard F. Shuman], FWS, Seattle, WA, to Mark Meyer. Located at NARA, Anchorage, AK.

12 Letter (16 Aug. 1946) from Willis H. Rich, Consultant, Salmon Fisheries Investigations, Stanford University, to R. F. Shuman, FWS, Seattle. Located at NARA, Anchorage, AK.

13 Memo (23 Oct. 1947) from Richard F. Shuman, Aquatic Biologist, to Seton Thompson, Division of Alaska Fisheries. Located at NARA, Anchorage, AK.

14 1) Bevan, Donald E. 1951. Karluk Lake stream surveys, 1948–1951. Kodiak Island Research Group, FRI, University of Washington, Seattle. Unpubl. report. 45 p.

2) FRI. 1948. Kodiak Stream Survey. Kodiak Research Committee, FRI, University of Washington, Seattle, WA. Unpubl. handwritten notes and maps.

3) FRI. 1949. Measurements, 1948–1956. Kodiak Research Committee, FRI, University of Washington, Seattle, WA. Unpubl. data.

4) FRI. 1949. Spawning ground measurements, red salmon, pink salmon, 1948. Kodiak Island Research, FRI, University of Washington, Seattle, WA. Unpubl. data.

5) FRI. 1949. Cannery measurements, red salmon, pinksalmon, 1948. Kodiak Island Research, FRI, University of Washington, Seattle, WA. Unpubl. data.

6) FRI. 1949. Cannery graphs, red salmon, pink salmon, 1948, 1953. Kodiak Research, FRI, University of Washington, Seattle, WA. Unpubl. data.

7) FRI. 1949. Spawning ground graphs, red salmon, pink salmon, 1948, 1949, 1950, 1951, 1952 (includes weir escapement). Kodiak Research, FRI, University of Washington, Seattle, WA. Unpubl. data.

8) FRI. 1954. Spawning ground measurements, 1950. Kodiak Island Research, FRI, University of Washington, Seattle, WA. Unpubl. data. 107 p.

9) FRI. 1954. Spawning ground measurements, 1951–1956. Kodiak Island Research, FRI, University of Washington, Seattle, WA. Unpubl. data.

10) Walker, Charles E. 1955. Scale analysis, 1948–1953. University of Washington, FRI, Kodiak Island Research. Unpubl. report.

11) Walker, Charles E. 1956. Age analysis of the Karluk red salmon runs, 1922, 1924–1936, and 1952–1955. FRI, University of Washington, Seattle, WA (January 31, 1956). Unpubl. report. 29 p.

All located at FRI Archives, University of Washington, Seattle, WA.

ulations to lend credence to Thompson's 1950 theory of the decline of the Karluk River sockeye salmon. Bevan and Walker found such evidence, but it was not formally published.

Rounsefell's One-Population Hypothesis

In a comprehensive analysis of factors causing the decline of the Karluk River sockeye salmon, Rounsefell (1958:135) made a statement that attracted great attention: "In summary, the evidence strongly indicates that the Karluk sockeye salmon comprise one population..." He gave two reasons in support of his statement: 1) the seasonal modes of abundance could be caused by the seasonal pattern of life history types, and 2) the numbers of early- and late-running 5_3 fish were correlated, as were 4_3 and 5_3 fish of the same year class. Ricker (1972:41) questioned Rounsefell's interpretation:

> [Concerning Karluk River sockeye salmon subpopulations] As I see it, however, none of the information presented precludes the possibility of considerable discreteness of stocks arriving at different seasons, provided the stocks are distinguished by having different proportions of the different life-history types, as is actually the case (personal communication from Dr. J. B. Owen). The fact that different ocean groups (having the same number of fresh water years) vary in abundance in a similar fashion might reflect variations in survival conditions in the Lake during their common freshwater life.[15]

Regardless of how one felt about Rounsefell's one-population hypothesis, there was no argument about the fact that he stimulated further research, because five relevant investigations followed.

After 1958: The Recent Era

In a thought-provoking paper detailing one possible explanation for the decline of the Karluk River sockeye salmon, and while not specifically referring to subpopulations, Owen et al. (1962) presented information that supported the existence of such entities. For example, they showed that the age composition of spring spawners (mainly ages 5_3's and 6_3's) was different from that of fall spawners (mainly ages 5_3's and 6_4's). Further, since age is determined largely by heredity (Godfry, 1958) and because sex ratio, size, and fecundity are dependent on ocean age, Owen et al. (1962) presented evidence of spring and fall subpopulations.

A second investigation (actually two independent studies) inspired by Rounsefell's one-population hypothesis was conducted at Karluk Lake in 1961 (Hartman and Raleigh, 1964). In one study, 200 adult sockeye salmon were caught in a weir trap as they tried to enter Meadow Creek, a lateral stream of Karluk Lake (Fig. 1-5). These fish were tagged, divided into experimental and control groups, and placed back into the lake. When they tried to reenter Meadow Creek, experimental fish were repeatedly returned to the lake, but control fish were placed upstream. Daily stream surveys for tagged fish were made at other spawning tributaries to record the movement and utilization of these areas by the experimental and control fish. Surprisingly, no greater than 3% of the experimental group spawned in streams other than Meadow Creek, and 79% repeatedly tried to enter Meadow Creek. The average number of attempts at reentering Meadow Creek was 11 per fish.

In their second study, an attempt was made to condition the returning adults into accepting a particular spawning tributary. In this study, 600 sockeye salmon adults were captured at the Karluk River weir trap near the lake outlet, divided into three groups, and tagged. The control group was released immediately at the weir, but the two experimental groups were put in pens and towed halfway to Grassy Point Creek on the west shore of Karluk Lake. One pen was then towed back to the lake outlet where the fish were retained, while the other pen was towed to Grassy Point Creek where the fish were held under the influence of that creek's water. After one control fish was observed during the regular stream surveys, all experimental fish were released and their subsequent appearances on the spawning tributaries were noted. Tag recoveries at Grassy Point Creek weir showed that fish held off that stream's mouth did not enter the tributary in greater frequency than did fish in the other two groups. This investigation proved that Karluk River sockeye salmon homed to specific spawning tributaries, conditioning after the fish entered the lake did not alter this tendency, and straying from the home stream was less than 3%.

Another study, designed to test whether lakeward migrations of Karluk River sockeye salmon fry were under genetic control, was carried out by Raleigh (1967) during 1965–66. Eggs were obtained from spawning sockeye salmon in the upper Karluk River, Meadow Creek (a lateral stream), and Thumb Beach at Karluk Lake (Fig. 1-5). After being fertilized, eggs were flown to a hatchery where they were incubated under identical conditions. When the fry hatched, their upstream or downstream movements in a simulated stream chan-

[15] A similar statement appeared in an earlier paper by Ricker (1959).

nel and time of day were noted. Migration direction (upstream or downstream) and timing (day or night) differed significantly between fry from Meadow Creek and those from Karluk Lake outlet. Fry from Thumb Beach behaved similarly to those from the tributary. The different behaviors were concluded to have a genetic origin, because the three lots were treated similarly during all phases of the study.

A fourth investigation by Wilmot and Burger (1985) was designed to determine if there were biochemical differences between groups of spring-run fish, groups of fall-run fish, or spring- and fall-run fish in the Karluk River system. Tissue samples were collected from spring-run fish spawning in Canyon and Moraine creeks and Upper Thumb River and from fall-run fish in Lower Thumb and O'Malley rivers. These samples were subjected to starch gel electrophoresis. Significant differences in allele frequencies of three enzymes were found between spring and fall runs, but no differences were found between groups of spring-run fish or between groups of fall-run fish. This evidence showed that the spring and fall runs of Karluk River sockeye salmon were genetically distinct entities (subpopulations), but it does not preclude the existence of additional subpopulations within the spring and fall runs.

The fifth and last investigation stimulated by Rounsefell's one-population hypotheses was by Gard et al (1987).[16] During 1962–65, morphometric, meristic, and age data from nine groups of spawning sockeye salmon and from spring and fall runs at the Karluk River weir were obtained, in addition to the timing, distribution, and abundance of sockeye adults on the spawning grounds. Further, the timing, abundance, and length of migrating fry in Canyon and Grassy Point creeks were determined. Statistically significant ($P < 0.05$) differences in freshwater and ocean ages, length, and fecundity of sockeye spawners, and in length of fry were demonstrated between spawning areas or seasons. Discriminant analysis using length, girth, fecundity, egg volume, and freshwater age showed excellent temporal (90% non-overlap) and moderate spatial (25% non-overlap) separation of spawners from different seasons or spawning areas. Based on the many studies cited above, Gard et al. (1987) concluded that at least part of each character difference found between the groups of sockeye salmon in their study was due to genetic differences. They demonstrated that the Karluk River sockeye salmon run was composed of at least two subpopulations that segregated by time and space.

[16] An earlier unpublished manuscript that utilized the same basic data reported here was prepared by Gard and Drucker (1972). Copy in personal papers of Richard Gard, Juneau, AK.

Discussion and Conclusions

The chapter title and paramount question to be answered is "Are Karluk River sockeye salmon differentiated into subpopulations?" The answer to that question is an unqualified "yes." Many anecdotal observations and scientific studies have produced evidence of the existence of subpopulations, but the fry behavioral study of Raleigh (1967) and biochemical genetic study of Wilmot and Burger (1985) proved their existence. Wilmot and Burger found significant differences in allele frequencies for enzymes from spring- and fall-run sockeye salmon, and since enzymes are the products of genes, these differences were genetic. Therefore, Rounsefell's one-population hypothesis was in error.

Why did Rounsefell (1958) run astray with his one-population hypothesis when most scientists either believed in the existence of subpopulations, or thought their existence highly probable? First, his correlation between the numbers of early- and late-running 5_3 fish and between 4_3 and 5_3 fish of the same year class would be compatible with a one-population hypothesis, but they do not prove that there was only one population. Ricker (1959) said these correlations might reflect survival conditions in the lake during the correlated groups' common fresh water life and, since he read Rounsefell's manuscript before it was published, he must have conveyed these concerns at that time. Further, Rounsefell must have known enough about the process of evolution[17] to realize that a variable species such as sockeye which, due to its homing instinct, is reproductively isolated on its spawning grounds in the complex Karluk River system, is likely to evolve into subpopulations given sufficient time.

Nevertheless, Rounsefell ignored Darwin, Ricker, Thompson, and many other biologists, and elected to interpret his data in an unlikely manner. Perhaps one reason that he erred was that he never carried out field studies of sockeye salmon at Karluk Lake. Scientists who have spent a few years at Karluk Lake, especially if they conducted regular stream surveys, have been impressed with: 1) the annual regularity (within a few days) of occupancy of the spawning habitats, 2) the diversity of spawning habitats, and 3) the extreme scarcity of fish between the two major runs. When one observes these phenomena, one thinks

[17] Mayr (1963) provides a thorough treatment of this process.

there must be some innate control of this precise and predictable process—and there is.

Resolution of the subpopulation question was important for two reasons. First, effective management could not be accomplished unless it was known whether or not the spring and fall runs were composed of two subpopulations or two groups of subpopulations. For example, the White Act of 1924 required that at least 50% of the entire run be allowed to escape to the spawning grounds. If there were only one subpopulation in the system, it might not matter what part of the total run was selected to supply the required escapement. However, if there were spring and fall subpopulations, it would matter a great deal. In the latter case, if the escapement came solely from the spring run, the fall run might easily be overfished and eventually cease to exist. Secondly, Thompson (1950) proposed a theory of the decline of the Karluk River sockeye salmon that was based on the existence of subpopulations (see Chapters 6, 11). Thompson assumed that subpopulations existed in the Karluk sockeye because of what he knew about genetics[18] and because subpopulations had been identified in other sockeye salmon systems. Many biologists accepted Thompson's theory and designed their investigations accordingly.

Since the subpopulation question was of major importance, why did the renowned biologists Charles Gilbert, Willis Rich, and Thomas Barnaby not investigate this question in the 1920s or 1930s? Perhaps they were simply too busy with other basic life history studies, or possibly they were already confident that subpopulations were present, making confirmatory studies unnecessary. Comments in their papers suggest that they tended to accept the existence of subpopulations.

Much evidence of Karluk River sockeye salmon subpopulations has never been published; it is found only in monthly reports, personal diaries, and correspondence. Other information exists as raw data, tables, or graphs located in weathered folders housed in various archives or personal libraries. This is true for much of the subpopulation work of DeLacy and Morton, Shuman and Nelson, and Bevan and Walker. This lack of publication and communication of previous subpopulation studies has caused much of this work to be duplicated by later researchers. One of the goals of this fisheries research history is to preclude unnecessary future duplication.

Finally, it has been proven that spring and fall subpopulations exist in the Karluk River sockeye salmon, and there is evidence that spatial subpopulations may also exist. We predict that future research will confirm the existence of one or more subpopulations on each principal spawning ground in the Karluk River system.

[18] Thompson, William F. 1963. Personal commun.

CHAPTER 6

Seasonal Run Distribution

They arrived from the sea in one huge wave—or two—or maybe three waves?

Before commercial fishing began in earnest at Karluk in 1882, what was the seasonal run distribution of its sockeye salmon? Was the original run distribution which existed when the Karluk ecosystem produced millions of adult sockeye drastically altered by commercial fishing? And, was the original distribution the same as has existed since 1921, when accurate measurements of the run began? These questions have persisted throughout much of Karluk's fisheries history, and with good reason. Knowing the original run distribution is important in understanding the true productive potential of Karluk's sockeye salmon and in making wise management decisions to sustain this natural resource. In this chapter, we review the different ideas about the seasonal run distribution of sockeye salmon at Karluk and summarize the historical evidence of the original run pattern that occurred before or shortly after commercial fishing started in 1882.

Before starting this review, some definitions are necessary. The term "escapement" defines the number of sockeye salmon that actually enter the Karluk River and migrate upstream to the spawning grounds. These fish escaped capture in the commercial fishery. Sockeye escapements have been accurately measured at the Karluk River weir ever since 1921; these measurements give detailed data on the seasonal run distribution (Fig. 6-1). Technically, the distribution determined by weir counts would differ somewhat from the true escapement distribution, as measurements would be affected by the time it takes sockeye to travel from the fishery until they pass the counting weir.

The term "catch" defines the number of sockeye salmon harvested in the commercial fishery. Catch numbers have been collected since Karluk's commercial fishery began in 1882, though their accuracy is questioned for some early years. Catch numbers for the early fishery were calculated from annual case-pack production records of the canneries, where one case of canned sockeye salmon equaled 48 1-lb (0.45 kg) cans. About 12–14 adult sockeye were needed to produce one case of canned salmon; the actual number varied seasonally as the size of returning salmon changed. Because seasonal catch or case-pack data have been recorded each year since 1882, these have often been used to reflect the seasonal run distribution.

The term "total run" defines the number of adult sockeye salmon that home to the Karluk River before they are reduced by commercial fishing. The total run is not directly measured in the ocean as these fish approach the Karluk River, but has been determined since 1921 by adding escapement and catch numbers. To determine the seasonal distribution of the total run, adjustments must be made between escapement and catch because of the time needed for salmon to travel from the fishery to the weir. Thus, weir counts must be adjusted back several days or weeks to match when the same group of fish was being harvested in the fishery. The following discussion on seasonal run distribution refers specifically to the total run. It is necessary to make this distinction since the term "run" is often used generally to refer to all types of fish migrations, including movements up the Karluk River and into specific spawning tributaries at Karluk Lake.

Present Seasonal Run Distribution, 1921–2010

Karluk's sockeye salmon run is somewhat unique in Alaska due to its length, from May to October, while many other sockeye runs only last a few midsummer weeks. Since 1921 seasonal records have been kept on the numbers of adult sockeye that migrate up the Karluk River (the weir counts) and on the numbers of salmon caught in the commercial fishery (Figs. 6-1, 6-2). Thus, the seasonal run distribution has been well known since 1921, especially when compared to the uncertainties of the previous 40 years. Of course, vast improvements have been made since 1921 in correctly assigning fish to the Karluk system. Information from

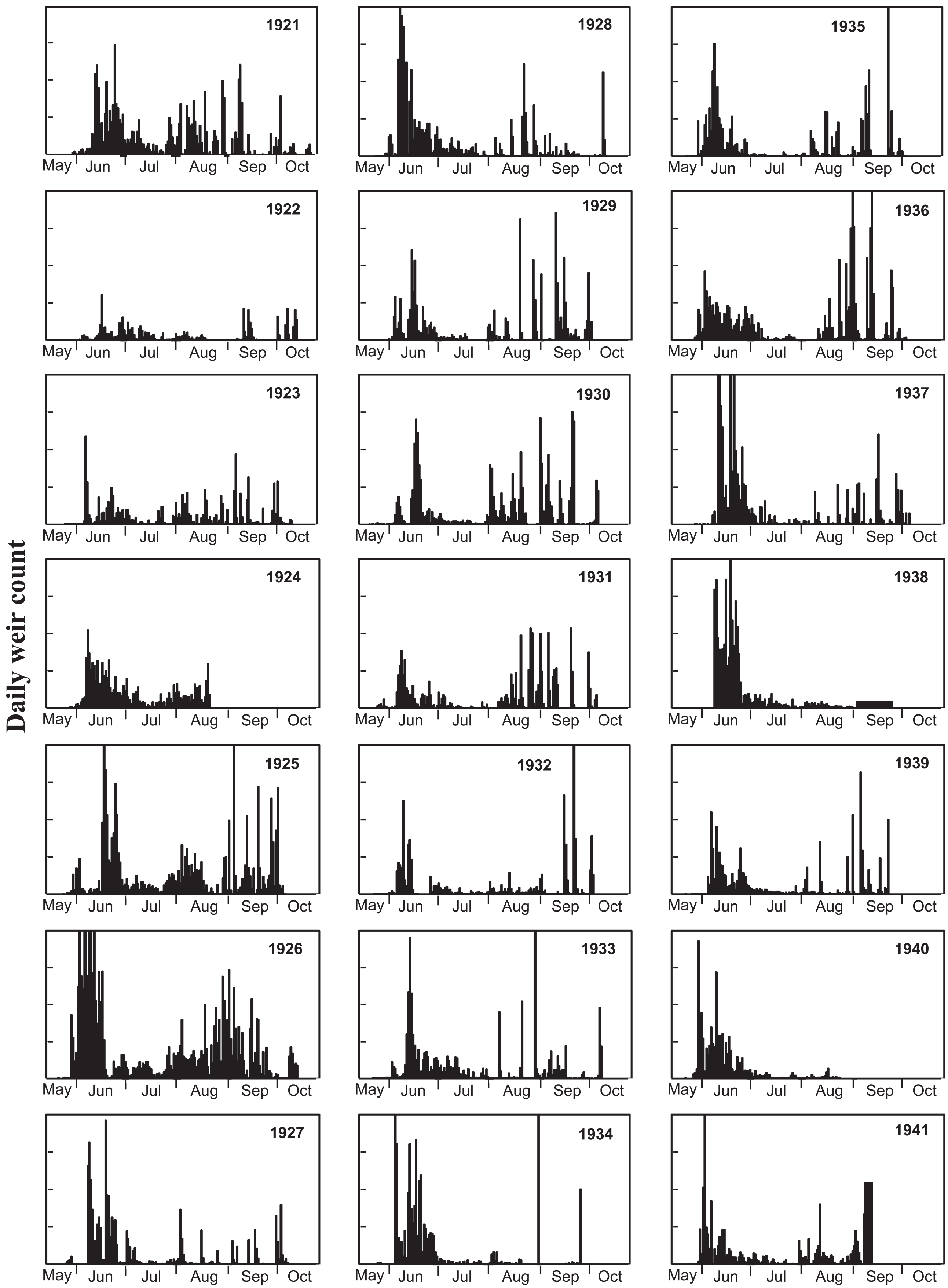

Figure 6-1 (A). Karluk River sockeye salmon daily weir counts, 1921–41. (Vertical scale: 0–80,000.)

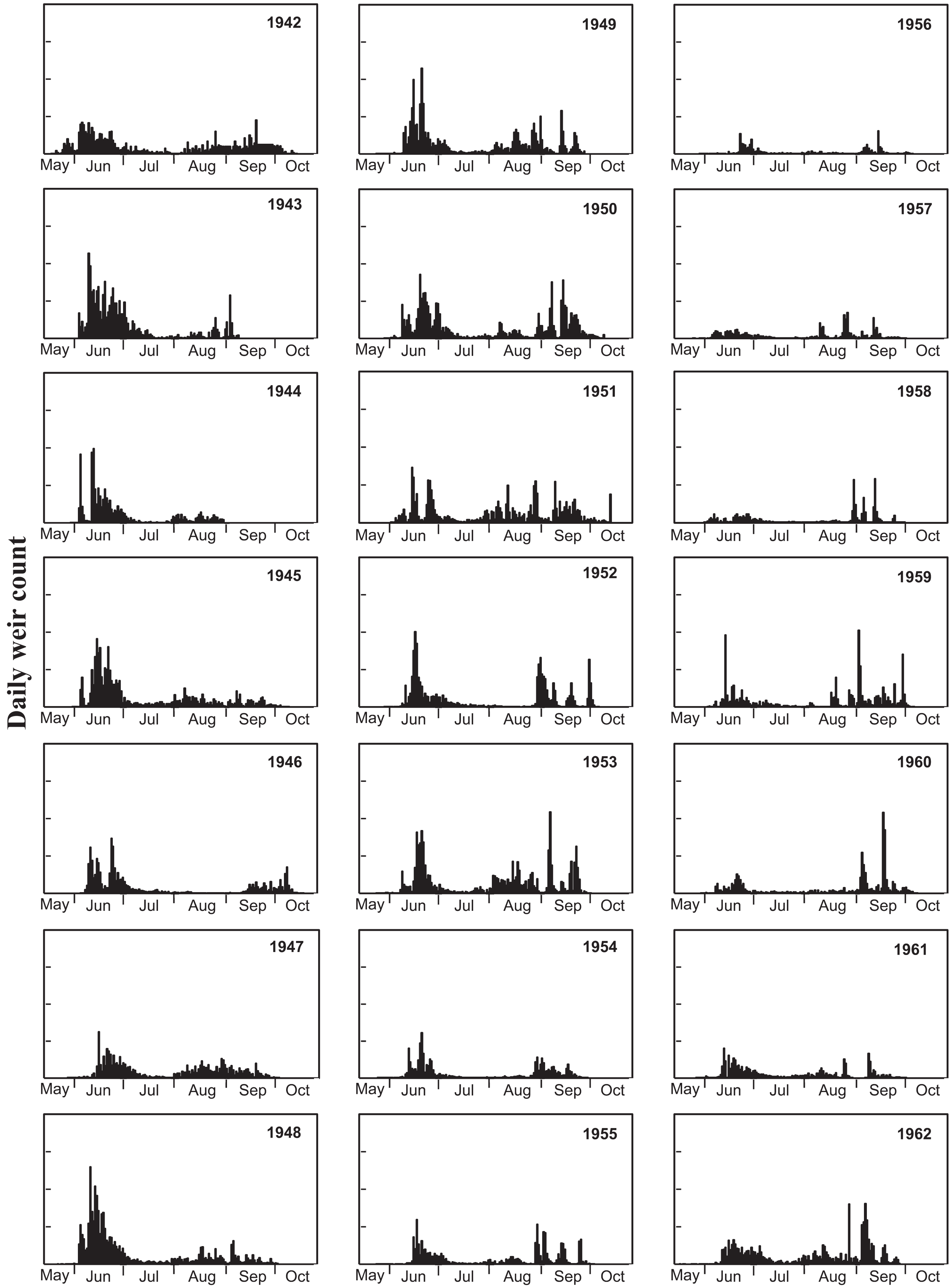

Figure 6-1 (B). Karluk River sockeye salmon daily weir counts, 1942–62. (Vertical scale: 0–80,000.)

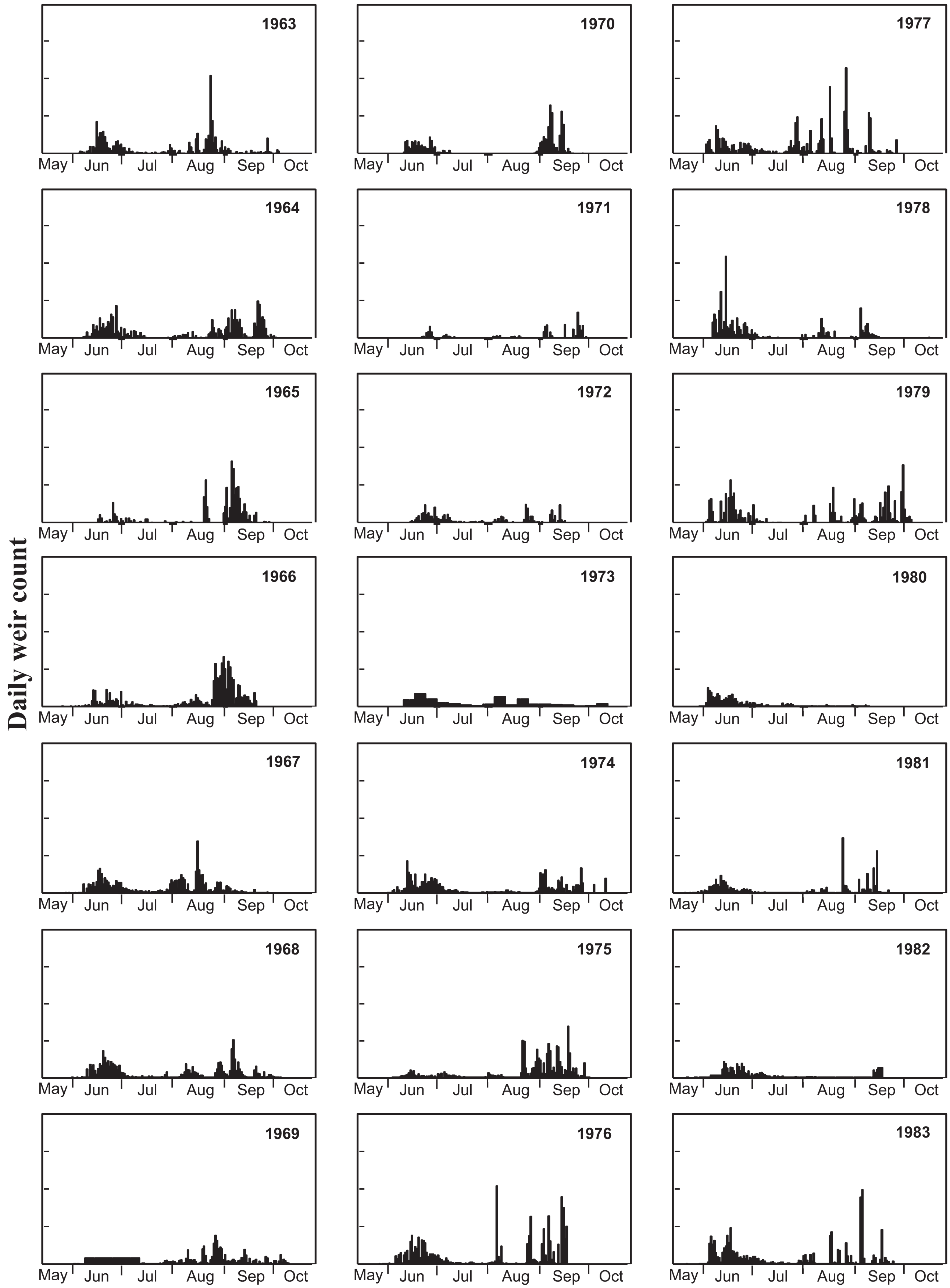

Figure 6-1 (C). Karluk River sockeye salmon daily weir counts, 1963–83. (Vertical scale: 0–80,000.)

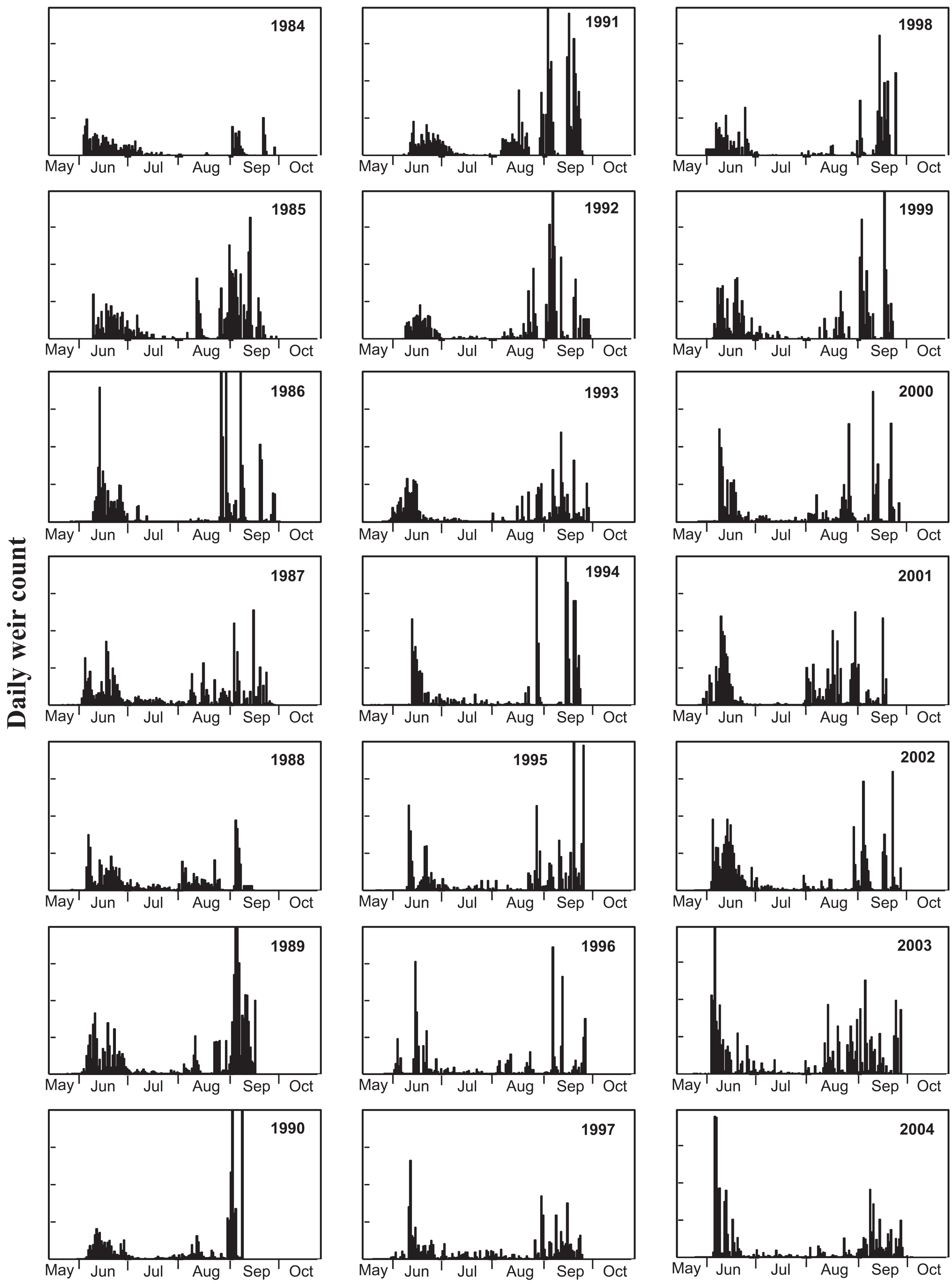

Figure 6-1 (D). Karluk River sockeye salmon daily weir counts, 1984–2004. (Vertical scale: 0–80,000.)

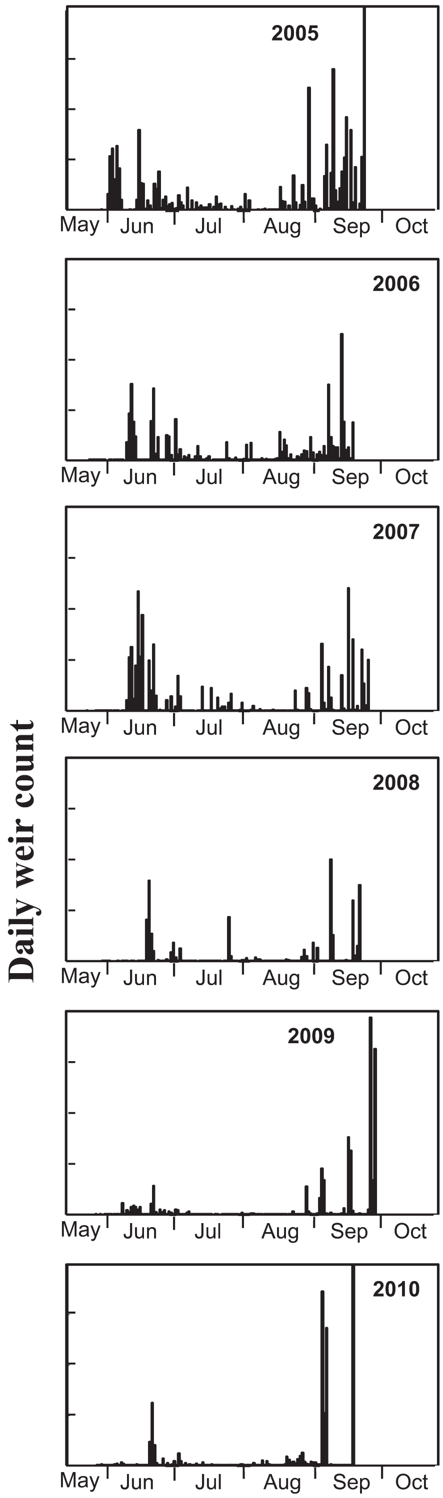

Figure 6-1 (E). Karluk River sockeye salmon daily weir counts, 2005–2010. (Vertical scale: 0–80,000.)

past ocean-tagging studies and run reconstruction methods that use age markers and scale analysis have reliably identified the true stock compositions of sockeye salmon that migrate along Kodiak Island's western coastline (Bevan, 1962; Witteveen et al., 2005).

Seasonal run distributions of Karluk's sockeye salmon have followed a relatively consistent pattern since 1921 (Figs. 6-1, 6-2). Typically, a few sockeye begin ascending the river in mid May and increase in abundance to an initial peak in early to mid June. Following this, the run gradually declines to a minimum in early to mid July. By late July the run normally increases again, reaching a second peak somewhere between early August and early September. The exact timing of the second peak varies from year to year. After the second peak, the run decreases through late September and into October. Rarely, the run continues into November.

Thus, sockeye salmon migration into the Karluk River has been bimodal since 1921, the two distinct runs often being called the "spring" (early) and "fall" (late) runs. These two runs are typically separated by a midseason low occurring about 15 July. Some fishery biologists have divided Karluk's sockeye migration into early (May–June), midseason (July–August), and late (September–October) runs (Thompson, 1950; Van Cleve and Bevan, 1973). For the following discussion, we use the terms "spring run" for the May–June mode, "fall run" for the July–October mode, and "midseason run" for the July–August part of the fall run.

Rounsefell (1958) claimed that Karluk's sockeye run was trimodal, with the first peak in early to mid June, the second peak in early August, and the third peak in early September. Barnaby (1944) also found an apparent trimodal run distribution, but stated that in any individual year it was bimodal. He believed that the trimodal pattern was caused by averaging the distributions of several years, with the fall peak occurring in late July or early August in some years and in early September in other years. It remains unknown why the fall peak varies by as much as a month, while the spring peak consistently occurs at the same time each year. Perhaps flow conditions in the Karluk River may either speed or retard the fall-run's ascent. Or, if serious errors existed in the travel time estimates between the fishery and weir, the apparent first peak of the fall run may be produced by catch data, while the apparent second peak may be produced by weir counts.

While Rounsefell and Barnaby analyzed the sockeye run distribution at Karluk for the years before 1951, Barrett and Nelson (1994) analyzed its escapement

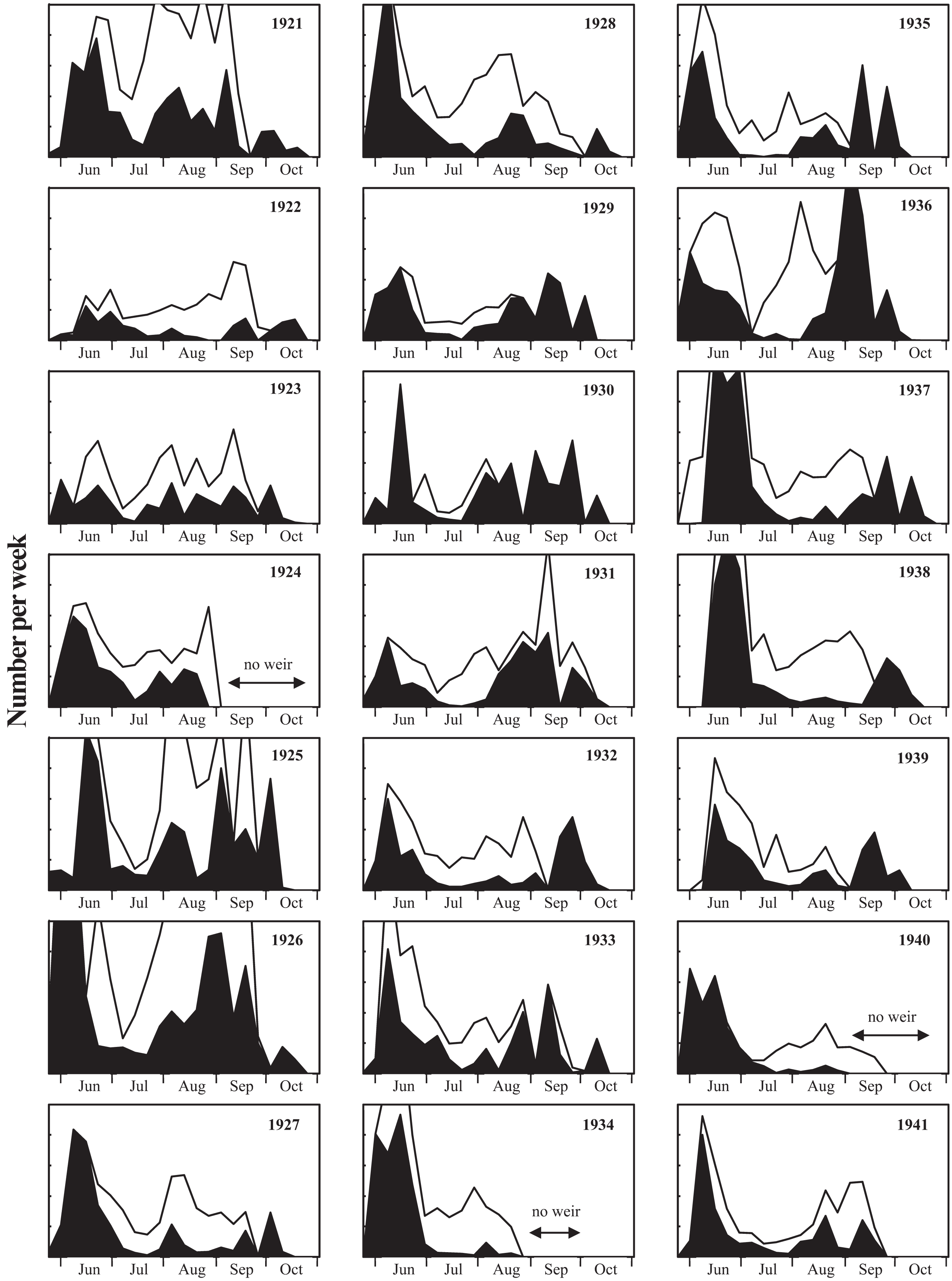

Figure 6-2 (A). Karluk River sockeye salmon weekly escapements (black area of graph) and catches (white area of graph), 1921–41. (Vertical scale: 0–250,000.)

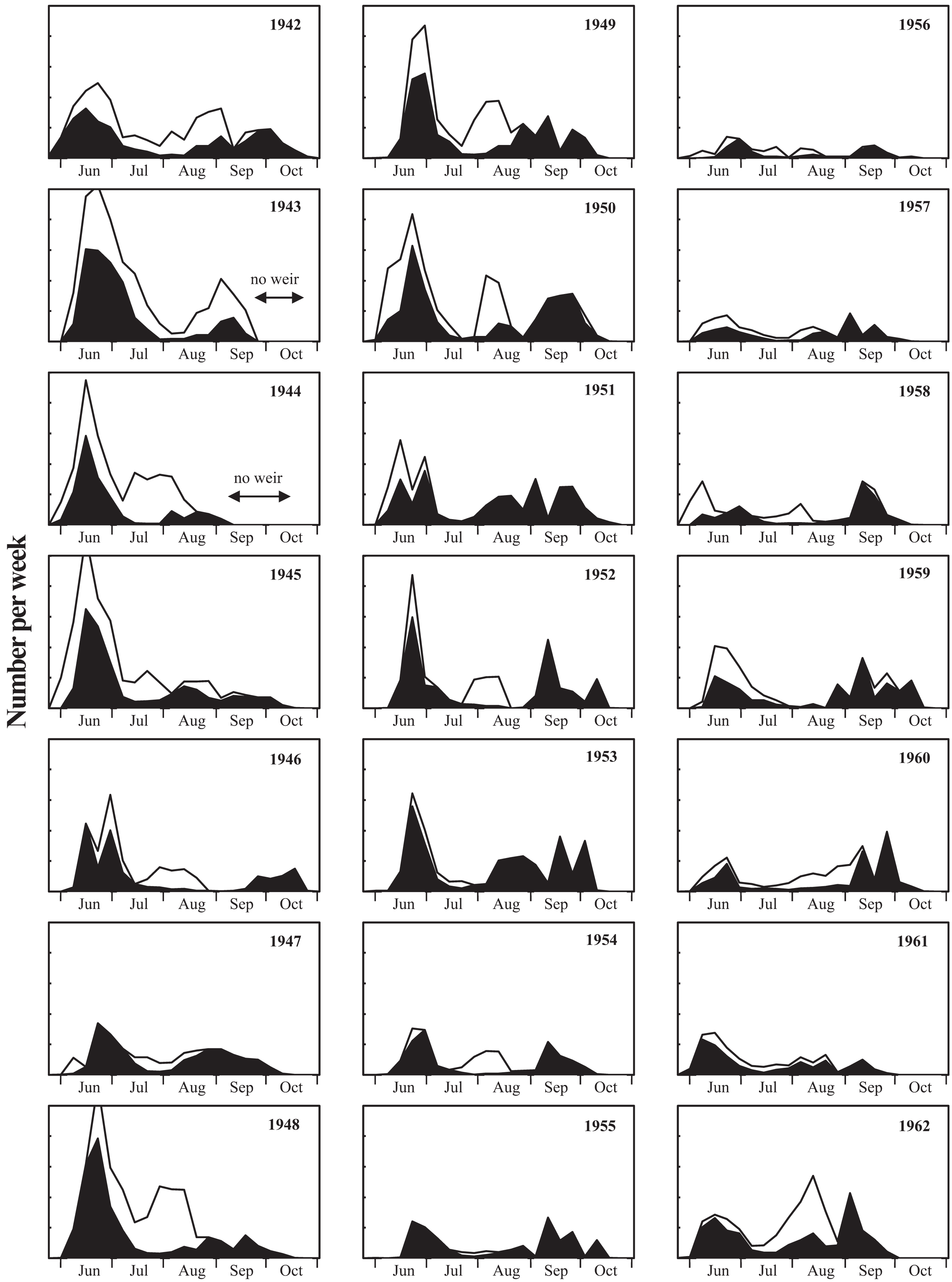

Figure 6-2 (B). Karluk River sockeye salmon weekly escapements (black) and catches (white), 1942–62. (Vertical scale: 0–250,000.)

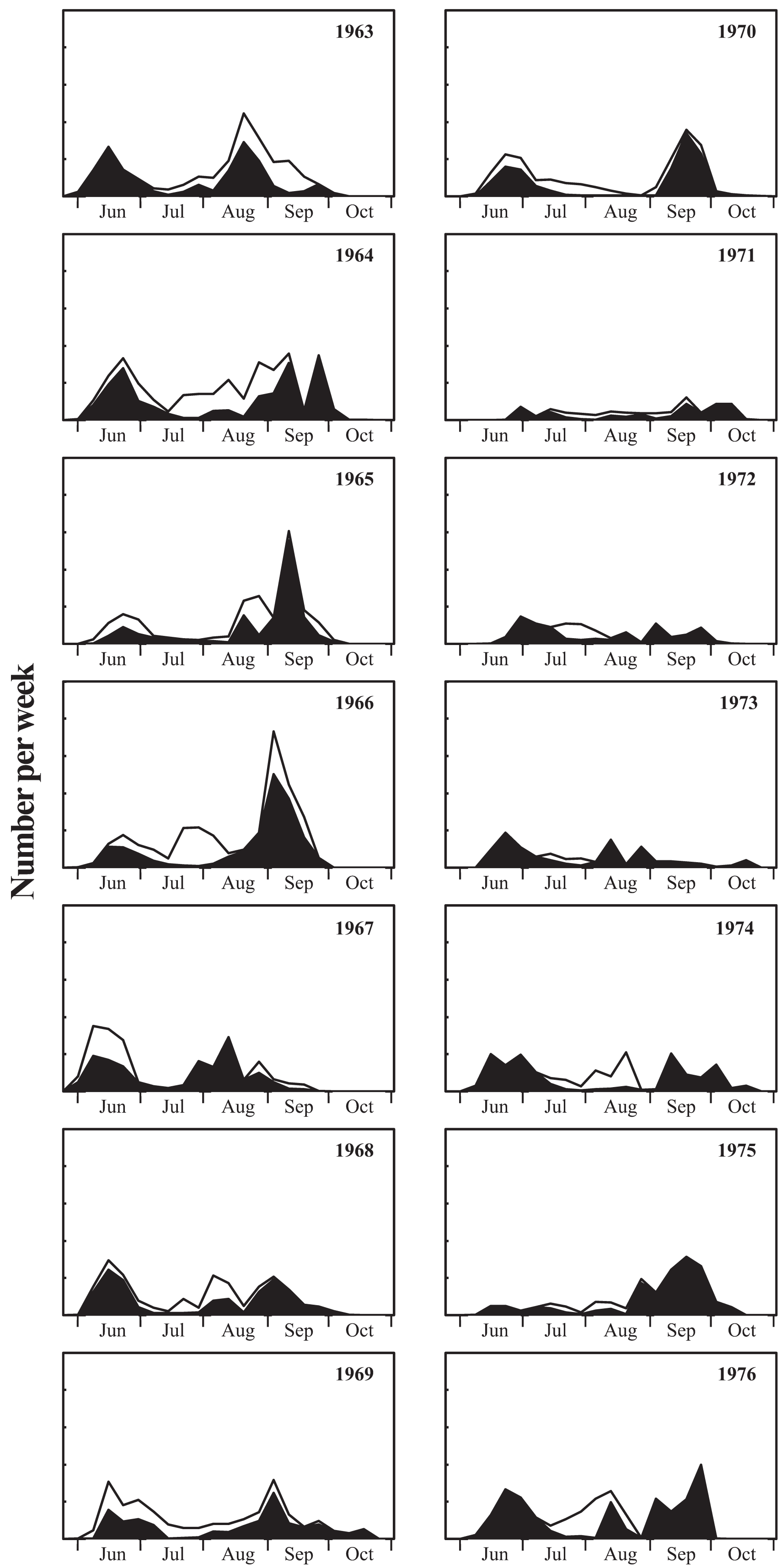

Figure 6-2 (C). Karluk River sockeye salmon weekly escapements (black) and catches (white), 1963–76. (Vertical scale: 0–250,000.)

data for 1984–93 and found a bimodal seasonal pattern with little evidence of trimodality. Their 1984–93 escapement pattern matched that of 1921–36, with an initial peak in mid June, a minimum in late July, and a second peak in early September (Barnaby, 1944; Thompson, 1950). The main difference in run distribution between these two eras was the broad fall-run peak during 1921–36 and the sharp peak during 1984–93. Perhaps the intense commercial fishery that continued for many years on midseason (July–August) sockeye sharpened the bimodal pattern of the run and escapement.

The present bimodality of Karluk's sockeye salmon run also exists, with appropriate lag times, at the counting weir and then again at the spawning grounds at Karluk Lake. When the weir was located near Karluk Lagoon (1921–41, 1976–2010), spring and fall peaks typically occurred at the weir a few days or weeks after the fish escaped the fishery. But when the weir was located 40 km upstream near the lake's outlet (1945–75), it took at least 7–10 days for sockeye to ascend the river from Karluk Lagoon, causing spring and fall escapement peaks to occur later than in the fishery. Since adult sockeye spend one month maturing in Karluk Lake before spawning, peak numbers do not occur at spawning sites for over a month after they escaped the fishery. Thus, spring-run sockeye first appeared on the spawning grounds in late June, increased to maximum numbers in the second or third week of July, and completed spawning in late July and early August (Fig. 6-3). By mid August, few spawning sockeye were present. Fall-run sockeye began occupying their spawning habitats in late August and reached peak abundance in mid or late September.

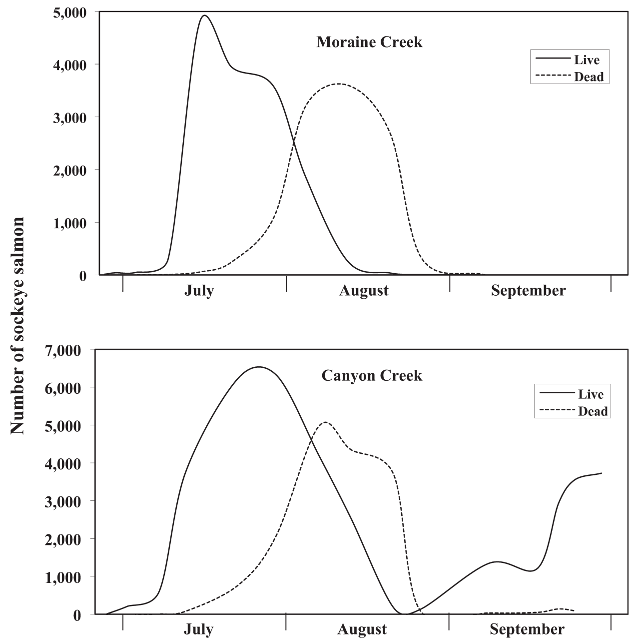

Figure 6-3. Live and dead adult sockeye salmon in a lateral tributary (Moraine Creek, 1953) and a terminal tributary (Canyon Creek, 1953) of Karluk Lake (from Bevan and Walker, 1954).

William F. Thompson's Ideas on the Original Seasonal Run Distribution

Because the seasonal run distribution of Karluk River sockeye salmon has been so consistently bimodal since 1921, this may, in fact, be the original run pattern that has always existed, as determined by the sockeye's evolutionary history and environmental adaptations to the Karluk ecosystem. Yet, FRI Director William Thompson proposed in 1950 that Karluk's bimodal run was not a natural biological feature of its sockeye, but instead reflected intense commercial fishing, especially in the early years when such fishing operated with few regulations or controls. He claimed that Karluk's original sockeye run was unimodal and reached maximum abundance in the midseason (July–August).

Thompson reached this conclusion by studying the seasonal case-pack records of one Karluk cannery for 1895–99 and finding that production was unimodally distributed. He assumed that case-pack records reflected the actual run distribution of sockeye salmon. Abundant midseason fish were assumed to be the most productive, while earlier and later runs were thought to be less productive. As he examined the cannery records of subsequent years (1900–19), the unimodal distribution progressively became bimodal. Hence, he concluded that commercial fishing on midseason fish had depleted this particular run segment and changed the seasonal run pattern from unimodal to bimodal. If true, loss of the productive midseason fish may then explain the historic decline in abundance of Karluk's sockeye salmon.

Thompson's ideas on run distribution came from his belief that Karluk's sockeye salmon had many independent subpopulations and that fishing could be intense on some subpopulations, while others went unfished. Thus, commercial fishing might alter the relative abundance and population dynamics of the subpopulations present. Since he felt that Karluk's fishing regulations protected early- and late-run sockeye, but allowed intense midseason fishing, he proposed changes to the fishing effort (Thompson and Bevan, 1955). Ideally, all subpopulations would get some pro-

tection to help sustain the full diversity of Karluk's sockeye salmon.

Thompson did not personally conduct field research on Karluk River sockeye salmon, but in 1950 he actively directed the Karluk field studies of other FRI biologists and had a keen interest in solving the problem of its declining runs. He first presented his run distribution ideas to the National Research Council, Washington, DC, on 9 November 1950, in a paper entitled "Some salmon research problems in Alaska."[1] The main points he made in the paper were:

1) Sockeye salmon runs are made up of many independent subpopulations.
2) Subpopulations allow a species to survive many environmental conditions.
3) Subpopulations use different parts of the stream and lake for spawning, and at different times.
4) The seasonal run distribution reflects the relative mortalities that salmon have experienced.
5) The most productive parts of the run are the most abundant and have the best survival chances.
6) Fishermen want to operate when fish are most abundant.
7) Fishing modifies the run distribution.
8) Regulations don't protect the most productive part of the run; the best part gets depleted.
9) Regulations only protect the early and late runs; the midseason run gets depleted.
10) Fishing and regulations changed the run distribution from unimodal to bimodal.
11) Ideal regulations would protect all subpopulations.
12) Sockeye salmon are resilient to heavy fishing pressure.

Influence of Thompson's Ideas

Thompson's idea—that Karluk's sockeye salmon originally had an abundant midseason run that was progressively depleted by commercial fishing—had a powerful influence on fishery biologists and managers for at least the next 20 years. Field studies during the 1950s–1960s were often focused on the relative productivities of spring-run, midseason, and fall-run fish. Managers adjusted fishing regulations and discussed ways to rebuild the midseason run. Further, Thompson's idea that Karluk's sockeye had many independent subpopulations also stimulated field biologists to look for evidence of these different run segments.

Thompson had a great influence on the research topics and methods of the FRI biologists who were then studying Karluk's sockeye salmon. In particular, Donald Bevan focused his 1950–58 field work on gathering sockeye subpopulation data from different run segments; determining the specific spawning habitats used at Karluk Lake by early, midseason, and late runs; and learning which subpopulations the commercial fishery harvested. He also examined historic case-pack records to see if the unimodal midseason peak observed in the early data had been incorrectly caused by non-Karluk fish being transported to Karluk's canneries for processing. Many years after Bevan ended his Karluk field studies, he continued to support Thompson's ideas (Van Cleve and Bevan, 1973).

Thompson's ideas about sockeye salmon had considerable influence beyond the FRI. During the 1950s, his ideas on subpopulations and run distribution caused the FWS to change their sockeye research program and fishing regulations at Karluk. FWS biologists readily accepted that sockeye subpopulations existed, but they questioned his ideas on the original run distribution and the impact of commercial fishing. Based on tagging studies done during 1946–48, FWS biologists Nelson and Shuman understood the seasonal run distribution and where different sockeye subpopulations spawned at Karluk Lake. Shuman felt that Thompson's case-pack data inaccurately reflected the seasonal run pattern and believed that the run had always been bimodal. Nelson also questioned Thompson's ideas on run distribution, but in 1955 planned field studies to test the relative productivities of spring, midseason, and fall-run sockeye:

> [Concerning the research program on Karluk River sockeye salmon, 1955] Dr. W.F. Thompson has stated that the middle portion of the Karluk escapement is more productive than the spring or fall section of the escapement. He bases this on the catch curves of a cannery at Karluk during the years 1900–1905. He believes the decline in the middle section of the run has been the fault of the F. & W. S. He claims this segment of the run has not been given adequate protection. It would appear that we must determine if the middle portion of the escapement is more productive now, and if so, the reasons why this is the case. To do this, we could construct a two-way weir on a stream like Canyon Creek. On this stream, fish from all segments of the escapement spawn. The survival of fish to the fry stage from

[1] Although this oral paper was never formally published, it was issued as FRI Circular Number 11.

> each group might be determined by various methods. The survival of fish to the fry stage from each group to the downstream migrant stage and to the adult stage might be measured by a large marking program in which fish from each group were marked with different fin combinations. From such a program we should be able to measure mortalities to the fry stage and to the migrant stage of fish in each group. Also, it might be determined if fish from each portion of the escapement at Canyon Creek return to the creek at the same time as their parents.[2]

Although Nelson never pursued this productivity research, he questioned the claim that midseason sockeye were the most productive. Yet, the FWS modified its fishing regulations in the 1950s to better protect midseason sockeye and attempted to rehabilitate this run segment (Van Cleve and Bevan, 1973). BCF biologists devoted considerable effort during 1957–70 to determining the relative productivities of Karluk's spring, midseason, and fall-run sockeye and the qualities of their spawning habitats.[3]

Challenges to Thompson's Ideas on Seasonal Run Distribution

Thompson presented powerful evidence that sockeye salmon at Karluk originally had a unimodal run distribution and that intense commercial fishing on midseason fish progressively changed it to bimodal. Case-pack data from one Karluk cannery during 1895–1919 demonstrated this change. Nevertheless, this interpretation can be tested further, particularly by considering whether historic cannery harvests accurately reflect the true run distribution of returning salmon. It is difficult to definitely prove or disprove Thompson's ideas on run distribution, but it is worthwhile to examine his assumptions and to consider additional evidence gained since 1950. In the following discussion we explore challenges to Thompson's ideas and pose some questions about the original run distribution.

Do Case-Pack Data Accurately Reflect the Seasonal Run Distribution?

Thompson's ideas about the seasonal run distribution of Karluk's sockeye salmon were based upon an important assumption—that case-pack production from one cannery during 1895–1919 accurately reflected the seasonal run pattern. Thompson did not test this assumption, though reasons exist for a poor correspondence between cannery production and run abundance.

Cannery Operations: It might be argued that the seasonal distribution of case-pack production in the early cannery years at Karluk at least partially reflected the necessary work of restarting operations in the spring after winter closure. This required a certain amount of time before fishing and cannery operations could began. Additionally, there were logistical problems of transporting men and supplies to this remote location. Thus, case-pack production in early spring may have been lower than it should have been based on the number of fish present. Once canneries were fully operational, every effort would be made to quickly meet annual production goals before the weather deteriorated in autumn. Case-pack data may then underestimate early spring sockeye runs and overestimate midseason and later runs. Likely, case-pack production was a combination of the intricacies of cannery operations, fishing effort, and sockeye salmon abundance.

A useful historical study would be to compare cannery startup times at Karluk Spit with spring run timing of sockeye salmon.

Fishing Effort: The seasonal distribution of case-pack production at Karluk's canneries may have partially reflected the commercial fishing effort. Historically, Karluk's sockeye salmon have been commercially harvested by four main fishing methods—beach seines, fixed ocean traps, purse seines, and gill nets. In the early fishery, most harvests were made with beach seines; ocean traps were first used in 1924. Although we know little about the seasonal habits and problems of commercial fishermen in Karluk's early history, seasonal weather differences alone probably caused fishing effort and efficiency to vary irregularly from May to October. Storms in Shelikof Strait often stopped commercial fishing for several days or weeks in the early years, allowing sockeye salmon unhindered access to the Karluk River. The manager of the Alaska Improvement Company, H. J. Barling, claimed in 1895 that at Karluk "about one-fifth of the entire fishing season is stormy, during which time it is impossible to "lay out" or haul a seine or net; but the storms do not prevent or obstruct the entrance of the fish" (Murray, 1896). Unimodal case-pack production in the early fishery may partially reflect better weather

[2] Letter (8 Nov. 1955) from Philip R. Nelson, Fishery Research Biologist, FWS, Seattle, WA, to Administrator, Alaska Commercial Fisheries. Located at NARA, Anchorage, AK.

[3] These studies were done by John B. Owen (1957–59), Robert F. Raleigh (1958–61), Benson Drucker (1961–70), and Richard Gard (1962–66).

conditions in midseason and poorer conditions in spring and fall.

As Karluk's sockeye salmon fishery developed, new fishing gear, improved methods, and larger boats may have allowed fishing to occur earlier and later in the year, making the bimodal run, if present, more obvious. Fishing effort was also affected by labor strikes that temporarily halted cannery operations and by governmental or self-imposed regulations on fishing times, locations, and methods. The proportion of sockeye salmon caught by different fishing gear (beach seines, purse seines, and gill nets) undoubtedly changed over the 25-year period (1895–1919) studied by Thompson. It remains unknown how these variations in fishing effort affected the seasonal case-pack production, but they may have been significant.

The historic changes in fishing effort for Karluk's sockeye salmon would be a worthwhile study. Pertinent data exist in many published and unpublished annual reports prepared by federal agents and wardens. Likewise, a valuable contribution to understanding the impact of commercial fishing on Karluk's sockeye salmon would be a chronological study of the 130 years of salmon fishing regulations.

Five-year Averages: Thompson used 25 years of case-pack data from one Karluk cannery to show that the sockeye's run distribution changed from unimodal to bimodal during 1895–1919. To do this, he averaged the case-pack data for 5-year periods: 1895–1899, 1900–04, 1905–09, 1910–14, and 1915–19. But using 5-year averages may obscure any natural bimodality present since peaks in the run often occur at slightly different times each year. Barnaby (1944) discussed the problem of using averages to understand the true run distributions during 1921–36. For example, he found that run distributions were bimodal each year, but the 16-year average was trimodal because of slight annual differences in run timing. While averaging errors may not be strong enough alone to invalidate Thompson's conclusions, they add doubt to this method of replicating run distributions. It would be valuable to reevaluate Thompson's thesis using case-pack data for individual years.[4]

Mislabeled Case Packs: Although Karluk's early canneries primarily packed sockeye salmon, other salmon species may have been canned and marketed under the same label as sockeye. We have little evidence of this deceptive practice at Karluk, but intense competition for sockeye salmon existed between canneries during the late 1880s and 1890s. Since cannery superintendents were expected to meet annual production goals, it would not be surprising if salmon other than sockeye were sometimes canned. The abundant runs of even-year pink salmon that flooded into the Karluk River in July–August may have been especially tempting to use as a substitute if the sockeye run was then in a midseason low. Canning midseason pink salmon as sockeye would tend to obscure any bimodality present in case-pack data. It is not idle speculation that this misleading practice may have occurred. In the 1904 report of the Alaska Salmon Commission, Jordan and Evermann discussed this problem of deceptively substituting one salmon species for another and recommended clearer standards for salmon canning labels.

Unidentified Salmon Species: Between 1882 and 1896 the total salmon catch at Karluk was not segregated by species (Rich and Ball, 1931). The entire catch was assumed to be sockeye salmon, but the numbers of other salmon species caught remained unknown. Potentially, pink and Chinook salmon may have contributed to the catch statistics, while late-running coho salmon and the small run of chum salmon contributed little. Thus, reported harvests of Karluk's sockeye may have been too high in the early years, and the seasonal distribution of case-packs may have been distorted by including other salmon species. Any bimodality in case-pack production would be completely obscured by pink salmon, which typically run in the midseason between spring-run and fall-run sockeye. Pink salmon runs occur exactly when Thompson claimed midseason sockeye salmon should be present. Pink salmon were considered to be undesirable fish during the early cannery years at Karluk (Roppel, 1986), but many were harvested during 1901–19 (Rich and Ball, 1931).

Salmon Imports to Karluk: Case-pack production during Karluk's early cannery years may have been supplemented by imports of sockeye salmon from other regions. Although these sockeye were not homing to the Karluk River, they were incorrectly added to its case-pack. Sockeye salmon homing to Chignik, Alitak Bay, Uganik Bay, Ayakulik River, and Little River were sometimes transported to Karluk's canneries. This practice altered Karluk's true case-pack data, which then falsely reflected the actual run distribution.

[4] This data is available on microfilm at the FRI Archives, University of Washington, Seattle.

Robert Porter (1893), Superintendent of the U.S. Census Office, mentioned that salmon from other areas were imported to Karluk's canneries in 1890, claiming that "steam tenders carry the fish from all outlying stations to Karluk." Moser (1899, 1902) visited Karluk's canneries in 1897 and 1900 and reported on importation of sockeye salmon:

> The canneries on Kadiak have prospected over this section and at times have sent a steamer to Kukak Bay and obtained a load of redfish.
>
> The canneries at Karluk are chiefly, but not entirely, supplied from the fisheries in Karluk Bight. A few fish are taken in the vicinity of Red River and Ayakulik, on the western side of the island, a few miles south of Seal Rocks; also off the Slide, the bluff next east of the spit; from the Waterfalls, about 3 miles to the eastward of Karluk, where two streams fall in cascades over a bluff; and from Northeast Harbor, a small indentation a few miles eastward of the Waterfalls; but these fish all belong to the Karluk school. Some years ago a few were taken at Little River, which is inside and a little westward of Cape Ugat, and from Kaguyak and Kukak, on the mainland. But all these places supply but a very small percentage of the Karluk pack. Occasionally, when there is a slack in the run at Karluk, one or the other of these places may be visited by the cannery steamer. Before the cannery at Uganuk was built the stream at this place was also fished by the Karluk canneries.
>
> In 1896 the Alaska Improvement Company packed 87,613 cases of redfish, 12 to the case. No other fish were packed and none salted or smoked. Of the above, 15,580 cases were fish taken at Uganuk, which ran 10 to the case; 3,500 cases from Ayagulik; 340 cases from Kaguayak, and 10 cases from Little River. The balance, 68,183 cases, were from Karluk beach and lagoon.
>
> The Karluk canneries this year fished the Spit and adjacent waters, Ayakulik, Uganuk, Little River, Eagle Harbor, and Kiliuda Bay, though the yield from the last two places was not over 9,000 fish.

Shortly after Thompson presented his ideas on the unimodal run distribution, Shuman claimed that case-pack data would not reflect the true run pattern of Karluk's sockeye because of fish imported from other areas:

> Dr. Thompson contends that the low between the spring and fall modes has been caused by overexploitation during that period, offering catch figures as proof. This is one more example of the errors introduced by unfamiliarity with the subject. It is true, as Dr. Thompson points out, early pack records from the Karluk Spit show a high pack during mid-July. What the records do <u>not</u> show is the origin of fish packed during that period. I have talked to many old-timers, fishermen, packers, and others, all of whom report that in those early days, the run at Karluk dropped almost to zero in mid-July, and during that period, fishing crews were moved to Uganik River, Red River, Little River, Olga Bay, Kaflia Bay, and sometimes Chignik. Fish were captured at these points, hauled to the Spit and canned there. Eventually, their identity was lost, and later generations came to regard them as having been Karluk fish. With this in mind, one must question seriously any statement to the effect that over-fishing "cut the heart out of the run."[5]

In 1953 Bevan further examined the early cannery records of Karluk and those from nearby areas to determine if sockeye had been imported to Karluk and added to its catch.[6] He particularly wanted to learn if midseason case packs came from other sources. If so, this would invalidate Thompson's claim of an original unimodal run distribution. Using the cannery records, Bevan corrected Karluk's case-pack data for the years 1899–1900 and 1906–13. He found that sockeye imports from Chignik and Alitak Bay were relatively minor, but transfers from Little River, Red (or Ayakulik) River, and Uganik Bay were significant in the early years, primarily in June–July. Few imports occurred in August–September.

Bevan concluded that imports affected case-pack data during early season, but not during mid or late season. Thus, Thompson's idea of abundant midseason fish remained intact. Nevertheless, for each of the 10 years Bevan examined, his corrections greatly increased the bimodality of case-pack data. Corrected case-pack data had an initial peak in mid June, followed by a low in early July, and then a second peak usually in August, but occasionally in late July or early September. Sockeye were imported when fish were scarce at Karluk and common elsewhere. Bevan's study demonstrated a bimodal distribution in Karluk's case pack, but also showed an abundance of midseason fish.

In addition to the inaccuracies caused by imported fish, how many sockeye were exported from Karluk without adding them to the case-pack data? The historic fisheries literature does report that exports were made to Chignik and Alitak in years of exceptionally large runs of Karluk River sockeye salmon (Moser, 1899).

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[5] Memo (7 Jan. 1953) from R. F. Shuman, FWS, Juneau, to Regional Director, FWS, Juneau AK. Located at ABL, Auke Bay, AK.

[6] Bevan, Donald E. 1953. The effect of red salmon catches from nearby streams on the Karluk pack. *In* Rae Duncan, Karluk, Packs of red salmon, 1895–1930. FRI, University of Washington, Seattle, WA (April 21, 1953). Unpubl. report. 26 p. Located at FRI Archives, University of Washington, Seattle.

Interception of Fish Homing to Other Areas: Sockeye homing to rivers other than Karluk may have been intercepted along Kodiak Island's coast and wrongly assigned to Karluk's catch during 1895–1919. Little was then known of the mixed-stock origins of harvested sockeye, and these fish were simply allocated to Karluk because it was Kodiak Island's largest run. Prior to 1889, sockeye were harvested in Karluk Lagoon and River, so their true origin was known. In 1889 commercial fishing moved to the ocean off Karluk Spit, and, gradually, harvests came from areas further removed from the Karluk River. Sockeye salmon homing to other Kodiak Island rivers and to Upper Cook Inlet are now known to pass through Shelikof Strait and along Kodiak Island's west coast during midseason. The true origins of these fish were not appreciated for many years (Rich and Morton, 1930; Bevan, 1959, 1962; Barrett, 1989; Malloy, 1988; Barrett and Nelson, 1994). Therefore, some intercepted midseason sockeye were likely added to Karluk's case-pack data, but, in fact, were not homing to that river. In the early fishery years when sockeye runs were abundant, significant numbers may have been intercepted and incorrectly included in Karluk's catch statistics. The addition of intercepted midseason fish would tend to obscure any natural bimodal pattern in the run. The ability of biologists to accurately assign catches of returning sockeye salmon to their true natal stream required a long learning process spanning much of the past century. Certainly, the accuracy of sockeye harvests at Karluk has varied substantially between 1882 and 2010, the data becoming much more reliable in recent years.

Abundance of Spring and Fall Sockeye Salmon During the July Lull: In Karluk's early fishery, when sockeye salmon were very abundant, spring and fall runs undoubtedly overlapped in July. Rutter mentioned this overlap in 1903, claiming "there are two distinct though intergrading runs, the first reaching its maximum about the last of June, the other the first of August."[7] Even with a July lull, sufficient fish may have been present in the early fishery to satisfy cannery demands. If true, case-pack production would reflect the peculiarities of cannery operations, not the seasonal run distribution. As sockeye abundance declined over the years, it is likely that July–lull fish became insufficient to meet cannery demands, and more fishing shifted onto the spring and fall peaks. Thus, case-pack data may have changed from unimodal to bimodal distributions even though the original run was bimodal.

Early Evidence of Bimodality: To show the shift from a unimodal to bimodal run distribution, Thompson studied case-pack data from 1895 to 1919. Bimodality was clearly evident in his 1900–19 data, but slight indications of bimodality also existed in his earliest data (1895–99). In these early years, when the overall run appeared to be unimodal, the distribution had a broad shoulder during June and early July that could be interpreted as the first of two modes. If true, this small early mode may have become more prominent as overall sockeye abundance declined. When Bevan studied Karluk's early cannery records, few data existed for the 1895–99 period, except for 1899. In that year case-pack output was bimodal after correcting for imported fish. Thus, even the earliest case-pack data showed some bimodality.

Case-Pack Data Prior to 1895: Thompson's main evidence of a unimodal run distribution at Karluk was the case-pack data from 1895 to 1899. Yet, by 1895 Karluk's commercial fishery had already operated for 13 years, and sockeye harvests had been extremely large for the previous seven years (1888–94), with annual catches often exceeding 3,000,000 fish. The cumulative harvest for 1888–94 was about 22,000,000 sockeye salmon. Sockeye catches remained high for a number of years after 1894, but it can be argued that by 1895 the fishery had already started to decline. Cannery data from 1888–94 may better reflect the original run distribution. Thus, the run distribution shown by Thompson's 1895–99 unimodal data may have already been changed after seven previous years of intense fishing.

Bimodal to Unimodal?: Directly opposite to Thompson's thesis, is it possible that intense fishing on Karluk's sockeye during 1888–94 had modified the run distribution by 1895 from bimodal to unimodal? With intense competition for fish, all run segments were likely harvested once canneries began operations each spring. To reach annual production goals as soon as possible, harvests may have focused on spring sockeye salmon, rapidly depleting their numbers. Reportedly, no sockeye salmon escaped to Karluk's spawning grounds in 1888 because a barricade was placed across the river in May–October (McDonald, 1889). Since the barricade was used

[7] Rutter, Cloudsley Louis. 1903. Field observations by Cloudsley Rutter on his Karluk work of 1903. Unpubl. notes. 48 p. Copy provided by Mark R. Jennings (Davis, CA) and located in Box 130, Barton Warren Evermann papers, Library Special Collections, California Academy of Sciences, San Francisco.

Karluk River sockeye salmon in spawning condition, male (bottom) and female (top). (Benson Drucker, Reston, VA)

Karluk River pink salmon in spawning condition, male (top) and female (bottom). (Benson Drucker, Reston, VA)

again in early 1889 (Bean, 1891), possibly all spring-run sockeye were harvested in 1888–89. Spring-run sockeye were abundant in the early fishery and anticipated by the canneries, but by 1895 cannery superintendents typically expressed disappointment when spring runs failed to return in abundance (Tingle, 1897). Poor spring harvests caused anxiety that the whole fishing season would fail, but usually the large August–September catches made each year a commercial success. While the above argument is speculative, it serves to illustrate the inherent weakness in using case-pack data to infer seasonal run distributions.

Test of Equivalence of Case-Pack Data and Run Distribution: Thompson apparently never tested the suitability of using case-pack data to estimate run distributions. Such a study could still be done, starting with 1921 since accurate data exist on case-pack production and run distributions for Karluk River sockeye salmon during that year. Also, many factors that affect cannery production, other than run abundance, may be similar to the early fishery years. These factors include cannery startups, operations, and goals, and fishing efforts and efficiencies as influenced by seasonal weather patterns. The case-pack and run data could be averaged over five-year periods to match Thompson's methods.[8]

In conclusion, considerable uncertainty exists as to whether historical case-pack data accurately reflect the true seasonal run distribution of Karluk's sockeye salmon during 1895–1919. During the early fishery there were many opportunities for errors in these data. Thus, the idea that the original run distribution shifted from unimodal to bimodal by commercial fishing is questioned. Most evidence suggests that an original bimodal run pattern existed, though midseason fish still may have been abundant.

Migratory Capacity of the Karluk River

Compared with other Alaska and Canada river systems that have bountiful salmon runs, the Karluk River is

[8] The Karluk case pack data for the years up to 1958 are present on microfilm at the FRI Archives, University of Washington, Seattle, or in APA cannery records.

not physically large. Does the Karluk River have a definite limit to the number of salmon that can ascend it at any one time because of the river's size constraints? Specifically, is it physically possible for two major salmon runs, the sockeye and pink, to simultaneously occupy the river during the midseason in July–August? Here, we investigate these questions as they relate to the original run distribution of sockeye salmon.

Thompson claimed that Karluk's midseason sockeye run was originally the most abundant and produced a unimodal run distribution. Historical records dating back to 1880, and recent weir counts, show that pink salmon ascend the Karluk River in July–August, being especially abundant in even-numbered years. If sockeye and pink salmon both reached peak abundance in midseason under natural pre-fishery conditions, then several million fish must have ascended the river simultaneously. In the early fishery years, Karluk's sockeye salmon runs often exceeded 3,000,000 fish and pink salmon runs in excess of 4,000,000 fish have been recorded. It is difficult to imagine that such large masses of salmon concurrently migrated up the Karluk River.

The Karluk River is typically about 90 m wide and less than 1 m deep.[9] Water discharge varies seasonally from about 3–60 m^3 per second (mean discharge is only 12 m^3 per second) (U.S. Geological Survey, 1974–82). Also, the river's flow regime is seasonally bimodal (Fig. 7-2). Discharges are low in winter, but then rapidly increase from spring snowmelt to a first peak in June. This is followed by declining flows through July–August, with often a low stage reached in late August. Autumn rains once again increase the discharge until a second peak is reached in October–November. Winter freezing and snowfall cause the river to recede in December–March. This seasonal bimodal pattern is again reflected in the water levels of Karluk Lake (Fig. 7-7).

If Thompson is correct about abundant midseason sockeye, then millions of sockeye and pink salmon must have migrated up the Karluk River in July–August in the early fishery years, just as river flows were declining and shallow water made upstream travel more difficult. This scenario seems biologically and physically unlikely. Indeed, some historical evidence shows that there are physical limits on the numbers of midseason salmon that can ascend the Karluk River at one time. Bean (1889) claimed that a huge pink salmon run prevented other salmon from entering the Karluk River in 1880:

> [At the Karluk River, 1880] Mr. Charles Hirsch, of the Karluk Packing Company, San Francisco, has recently described to us an unusual run of this salmon in Karluk River. About the 6th of July, 1880, a glut of humpbacks came into the Karluk and continued five weeks, during which time no other salmon could enter the river. It was impossible to pull a boat across the stream.

When Bean (1891) visited Karluk in 1889, he claimed that the river had no natural or artificial obstructions to salmon migrations, "unless we may regard the low summer stage of the water in such a light." In 1924, over 4,000,000 pink salmon ascended the Karluk River during the midseason low flows, and this horde of fish apparently overwhelmed the river's oxygen capacity and caused a massive fish kill:

> [At the Karluk River, August 1924] The large humpback run in Karluk River did considerable damage to the red salmon spawn. On August 21st hundreds of thousands of fish died in the twenty miles of river between the weir and the still water at the Larsens Bay Portage. The mortality included adult red salmon, humpbacks and trout as well as young fish. The cause is unknown unless it was due to overcrowding of humpbacks with a possible fall of water level in the river. Mr. Wood states that a few days later the river was still packed with live fish. There were over four million humps passed up through the weir.[10]

Comparing the size and flow characteristics of the Karluk River with the huge early runs of sockeye and pink salmon, it seems unlikely that two major runs could use the river in midseason. If physical limits exist in the river's migratory capacity, then the run timing of sockeye and pink salmon should be selected by a long evolutionary process to minimize overlap of the two species. Salmon migration patterns since 1921 show little overlap between bimodal sockeye runs and midseason pink runs. Further, pink salmon appear to be better suited than the larger sockeye for navigating Karluk's shallow midseason waters.

Considering the Karluk River's flow regime, it is striking that the migration peaks of spring- and fall-run sockeye salmon often coincide with high or increasing discharges. This correspondence is especially evident in spring-run sockeye, which peak just as the river crests in mid June. The peaks in fall-run sockeye

[9] Jefferson F. Moser, an APA official, gave testimony in 1912 at a U.S. Senate hearing on Alaska's salmon fisheries and declared that the Karluk River mouth was so narrow that "You can almost jump across it. It is not more than 50 feet . . . It is just a small stream" (U.S. Senate, 1912).

[10] Lucas, Fred R. 1924. Report of Kodiak-Afognak District for the month of September 1924, including the inspection of the Karluk and Uganik spawning areas. Afognak, AK (4 Oct. 1924). Unpubl. report. 9 p. Located at NARA, Anchorage, AK, and at ABL Library Files, Auke Bay, AK.

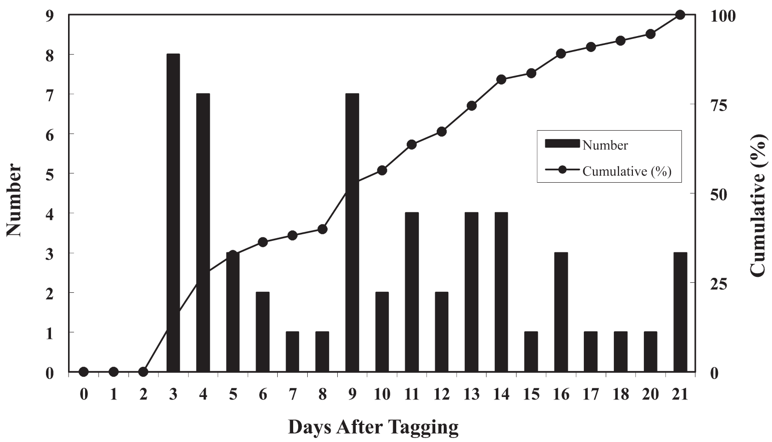

Figure 6-4. Travel time of adult sockeye salmon tagged in the ocean at Karluk Spit on 1 August 1925 until their passage of the lower Karluk River weir. Of the 200 tagged sockeye, 55 were observed at the weir (data located at NARA, Anchorage, AK).

and river flow match less precisely, the discharge being dependent upon the exact timing of autumn rains. Fall-run sockeye have difficulty ascending the Karluk River in some years because of low water, as shown by their longer travel times (Gard, 1973). Fall-run sockeye often linger in Karluk Lagoon for days or weeks and only begin their ascent after rainstorms cause the river to rise. Gard (1973) found a high correlation between fall-run sockeye escapements and rainfall, indicating a linkage between migration timing and water flow.

If sockeye and pink salmon were originally abundant in the midseason, pink salmon must have had difficulty establishing and defending spawning redds in the river during a major sockeye migration. Pink salmon spawning should be more efficient when few other river migrants are present, as occurs presently with the bimodal sockeye run. The midseason pink salmon run fits neatly between the spring and fall sockeye runs. Further, pink salmon can easily occupy the midseason spawning niche since their run timing, unlike sockeye salmon, is not linked to lake plankton blooms or a complex life history in freshwater. Thus, run-timing evidence of sockeye and pink salmon in the Karluk River does not support the idea that sockeye had an original unimodal run pattern with maximum midseason abundance.

Effect of Travel-Time Inaccuracies on Seasonal Run Distribution

The total run of Karluk River sockeye salmon is determined by adding weir escapement counts and commercial fishery catches. The catch for any particular day is added to the weir count made several days or weeks later. The lag between catch and weir count is caused by the time needed for escaping fish to travel from the fishery to the weir. To correctly measure seasonal run distribution, catch and escapement figures should come from the same group of fish being caught and escaping the fishery at the same time. To do this, true travel times must be known. Inaccurate travel times will distort calculated run distributions and times of peak abundance. In determining travel times of Karluk's sockeye salmon, it is important to distinguish the season and at least two travel segments: 1) from the fishery to Karluk Lagoon, and 2) from Karluk Lagoon to the weir. The weir was located on the lower Karluk River only 5 km from the ocean during 1921–41 and 1976–2010, but was located near Karluk Lake's outlet about 40 km upstream from the ocean during 1945–75.

Several biologists conducted travel-time studies on sockeye salmon early in Karluk's research history. Rutter tagged 400 spring-run sockeye and released them off Karluk Spit in 1903.[11] These fish entered the river within one day and few remained in the lower river after one week. They reached Karluk Lake in about 10 days. Gilbert tagged 200 sockeye salmon in the ocean off Karluk Spit on 1 August 1925 and recorded their weir passage.[12] These fish had a mean travel time between the ocean fishery and lower Karluk River weir of 9.7 days (range of 3–21 days), surprisingly long for the relatively short distance of only 5 km (Fig. 6-4). In mid July 1926, Gilbert tagged 100 sockeye

[11] See footnote 7.

[12] 1) Letter (18 Aug. 1925) from Ray S. Wood to Fred R. Lucas. Located at NARA, Anchorage, AK.
2) Letter (11 Sept. 1925) from Ray S. Wood to Fred G. Morton. Located at NARA, Anchorage, AK. Only 55 of the 200 tagged fish were seen to pass the weir and it is unclear what happened to the other 145 fish. Possibly, some tagged fish passed the weir without being detected and some may have remained for several weeks in Karluk Lagoon before moving upstream. Since sockeye salmon were counted through the weir until 6 October in 1925, any late-migrating tagged fish should have been seen.

salmon at the lower weir and recorded their passage at the Portage weir. These fish had a mean travel time of 4 days (range of 2–9 days) over the 20 km between the two weirs. Rutter and Gilbert's results suggested significantly different migratory behaviors for spring- and fall-run sockeye. Barnaby (1944) used 7-days of travel time when he calculated the total run during 1921–36; this became the standard figure used by biologists for many years, without adjustments for season or weir location.

After the weir was moved to Karluk Lake's outlet in 1945, Shuman and Nelson tagged adult sockeye and measured their travel times over the 35 km between upper Karluk Lagoon and the lake. Spring-run sockeye ascended the river in 6–7 days, but fall run fish needed 10–11 days (Gard, 1973). Shuman and Nelson did not measure the additional time that sockeye needed to travel from the fishery to upper Karluk Lagoon. Their results agreed with Rutter's over the same distance, but differed from Gilbert's findings that fall-run fish needed more than 10 days to reach the lake. In a 1949 tagging study, Bevan (1959, 1962) found that spring-run sockeye needed 9 days to travel from the fishery to Karluk Lake and discussed how slight changes in assumed travel time affected the calculated run numbers. When Walker and Bevan tagged midseason sockeye at Karluk Lagoon in 1952, these fish needed, on average, 21 days to reach the lake, much longer than the 6.5 days needed by spring-run fish.[13] Similarly, when Nelson and Abegglen (1955) tagged sockeye at Karluk Lagoon in June–August 1953, the later runs had longer travel times. Gard (1973) also found that sockeye tagged in August–September 1963 took much longer to ascend the river than did spring runs. Thus, despite some unexplained differences in these early tagging results, evidence was mounting that spring- and fall-run sockeye had different travel times.

After many years of using the standard 7-day travel time, the ADFG tested this assumption in 1970 by tagging adult sockeye in Karluk Lagoon and recording their passage of the weir at the lake's outlet.[14] They found that the 7-day travel time was reasonably accurate for spring-run sockeye, but fish tagged in July–August had mean travel times from 23 to 35 days. Incredibly, some midseason fish spent up to 54 days in the lagoon and river before they reached the lake. The ADGF study did not include the extra travel time between the fishery and Karluk Lagoon. More recently, Barrett and Nelson (1994) reported travel times for the 5 km between Karluk Spit and the lower weir as 5 days for early-run and 10 days for late-run sockeye, similar to Gilbert's 1925 results.

Clearly, the travel times of Karluk River sockeye salmon vary seasonally—spring-run fish quickly move up the river, fall-run fish need more time. Since most seasonal run distributions have been calculated using the standard 7-day travel time, substantial errors exist for midseason and later runs. These errors became obvious in 1970 when the ADFG calculated the sockeye run distribution using two different travel time methods: 1) the standard 7-day travel time assumption, and 2) their actual tag-determined travel times as measured in 1970.[15] Both methods showed a bimodal run distribution for Karluk's sockeye salmon, but large differences existed in the times of peak abundance. For the tag-determined method, the longer travel times in July–August shifted the peak run abundance about one month earlier than normally expected from using the 7-day method (i.e. from mid September to mid August). Also, the sharpness of the fall peak was substantially lowered, the sockeye run being spread over more time. Thus, the contrasting migratory behaviors of spring-run fish that quickly moved upstream and fall-run fish that lingered in Karluk Lagoon enhanced the bimodality of weir counts and spawning-ground use. These results suggest that the natural run of sockeye salmon in ocean waters as they home to the Karluk River also has a bimodal seasonal distribution, with a sharp spring peak and a broad fall peak.

The different travel times of spring- and fall-run sockeye salmon raise several questions. Why do midseason sockeye (July–August) have longer travel times than do spring-run sockeye? Are travel time differences innate to each run, or are they caused by environmental factors? What advantage, if any, is there for fall-run fish to remain for many weeks in Karluk Lagoon rather than proceeding directly to the spawning grounds? Are past errors in estimating travel time responsible for the reported trimodal run distributions of Barnaby (1944) and Rounsefell (1958), with the middle peak being caused by catch data and the later peak being caused by weir count data?

[13] Walker, Charles E., and Donald E. Bevan. ca. 1968. Factors possibly contributing to the condition of the Karluk sockeye salmon run. Unpubl. handwritten report. 18 p. Located at FRI Archives, University of Washington, Seattle.

[14] Simon, Robert J., Jack Lechner, Martin F. Eaton, Peter B. Jackson, and Louis A. Gwartney. 1970. Kodiak area management annual report, 1970. ADFG. Unpubl. report. Located at ASA, Juneau, AK.

[15] See footnote 14.

Two environmental factors may cause different travel times in Karluk's sockeye salmon: 1) seasonality of river discharge, and 2) pink salmon abundance. The Karluk River has a bimodal flow regime; the first peak occurs in June from snowmelt runoff, the second peak occurs in October–November from autumn rains. Snowmelt runoff is a predictable seasonal event each year, but the timing of autumn rains varies. Typically, low or declining river flows exist in July–August. Spring-run sockeye have short travel times because abundant river flows exist each June. These fish enter Karluk Lagoon and continue with little hesitation to the spawning grounds. Ascent of the river is relatively easy because of high flows and the absence of adult pink salmon.

In contrast, migratory conditions change substantially in July–August as flows decline and pink salmon enter the river, especially in even-numbered years. Sockeye salmon entering Karluk Lagoon in late July and August must now contend with low river waters and numerous pink salmon, both hindering free upriver migration. In abnormally dry years, the Karluk River can have very low flows that cause fall-run sockeye to hold in Karluk Lagoon for extended periods awaiting better conditions. This phenomenon has been observed many times by field biologists and weir tenders:

> [1897] . . . in many localities much depends upon the stage of water in the river. If the water is low, so the fish can not ascend, they are held in the salt or brackish water and do not seem to ripen so rapidly, but if there is sufficient water they do not remain around the mouth of the river very long, but pass rapidly to the lakes.
>
> [At Karluk, 1903] After entering the brackish water estuary, salmon play about for a day or two before continuing their migration up the river, and sometimes they remain in the estuary a much longer time. One tagged specimen was taken in the estuary a month after it had been released there, and several were taken as much as a week after tagging . . . The Karluk salmon are about ten days reaching the lake from the mouth of the river, which makes the rate about three miles a day.
>
> [At Karluk, 25 November 1921] During the latter part of the run the fish would stop over in the lagoon long enough for a red tinge to become noticeable on the skins of about half of them passing through the gates. The early part of the run, the fish were fresh and bright and were not observed schooling up in the lagoon.
>
> [At Karluk, 1923] The incoming fish displayed the same habits as heretofore in schooling up in the deep pool at the head of the lagoon until a large school gathers; then something starts them upstream in a body. Sometimes it seems to be a raise in the river, at other times there is no apparent cause. Old timers in the locality say that the fish always have acted so and it is especially noticeable during the latter part of the season.
>
> [At Karluk, 1926] About July 1 water became quite low as the snow fall last winter was very light and this summer rather dry. During August the river became very low and the salmon seemed rather reluctant to make the ascent, many staying in the lagoon until they became quite red. When the river would rise slightly they would at once commence to go up in numbers. . . . Red salmon continued to run steadily all through the month of September. An occasional rain would raise the river slightly making their passage easier.
>
> [At Karluk, 22–24 September 1935] We made a survey of the lagoon and estimate there are from 50 to 75 thousand fish here, many of them have become so weak they will never reach the Lake. Water very very low. . . . Heavy rain last night, river raised about two inches, had the largest run of fish for the season. Starting in to rain to night again. Expect we will clean lagoon of fish tomorrow. [16]

Besides the river's flow conditions, the presence of pink salmon apparently reduces the number of migratory pathways for sockeye. Pink salmon establish and guard spawning redds in the main river channel, and upmigrating sockeye must pass through these defended areas. Significantly, Walker and Bevan noted that abundant pink salmon in even-numbered years delayed upmigrating sockeye and reduced their vitality:

> [Speaking of Karluk River sockeye salmon, 1952] One further point, during the tagging of mid-run fish in Karluk Lagoon in 1952, the individuals were easily netted and presented no problem during the handling process connected with tagging. The behavior was very unlike that demonstrated by fish treated similarly on other occasions in the same general area. It would appear that in 1952, the heavy concentration of pink salmon affected the vitality of the sockeye salmon, which could have resulted in delayed upstream migration and/or mortality.[17]

Likewise, ADFG found in their 1970 study that sockeye tagged in July–August needed much longer

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[16] 1) Moser (1899).
2) See footnote 7.
3) Letter (25 Nov. 1921) from Fred R. Lucas, Fish Culturist, Parkplace, OR, to Henry O'Malley, Field Assistant, Seattle, WA.
4) Lucas, Fred R. 1924. Report of the red salmon census at Karluk Alaska during the season of 1923. Dep. Commerce, USBF. Unpubl. report. 4 p.
5) Hungerford, Howard H. 1926. Report of operations at Karluk Weir (Lower) season of 1926. Dep. Commerce, USBF. Unpubl. report. 4 p.
6) Hungerford Howard H. 1935 notebook. References (3)—(6) located at NARA, Anchorage, AK.

[17] See footnote 13.

times to reach Karluk Lake and suggested that pink salmon hindered their migration.[18] These midseason fish had higher mortalities than early-run fish. The ADFG proposed repeating the tagging study in 1971 to measure travel times in a year with few pink salmon, but this study was not done. We believe a comparative travel-time study between two years with drastically different pink salmon runs may give insights into the migratory behavior of fall-run sockeye. Such a study is appropriate since perusal of weir-count data suggests that fall-run sockeye change their migratory behavior between even- and odd-numbered years.

We contend that fall-run sockeye have longer travel times because of two environmental factors, water flow and pink salmon abundance, not because of innate features of these subpopulations. In years with high river flows and few pink salmon, fall-run sockeye arrive at Karluk Lagoon and proceed with little delay to the spawning grounds. In years when the ascent is harder, fish hold in Karluk Lagoon and only reach Karluk Lake with difficulty. These different responses to environmental conditions, which vary considerably from year-to-year, may explain why peak weir counts of fall-run sockeye vary from early August to early September. When environmental conditions are favorable, peak weir counts occur in early August; when conditions are unfavorable, peak weir counts occur later.

In summary, the calculated run distributions are distorted by errors made in estimating the travel times of sockeye salmon between the fishery and weir. These errors tend to enhance the natural bimodal distribution, since fall-run fish that have escaped the fishery may remain for several weeks in Karluk Lagoon before passing the weir. Seasonal distribution of weir counts is not the same as seasonal distribution of escapements. Natural environmental variations in river flow and pink salmon abundance affect the travel time of fall-run sockeye, while spring-run sockeye quickly migrate upstream. Because spring- and fall-run sockeye have different travel times between the fishery and lake, the run distribution becomes more bimodal once fish enter the Karluk River, as compared with their ocean migration along the coast of Kodiak Island. Travel time errors have caused midseason sockeye abundance to be underestimated, while abundance in September has been overestimated. This conclusion further brings into question the idea that intense fishing on midseason fish caused the bimodal run distribution. It suggests that depletion of midseason fish, in relation to the other run segments, has been less severe than indicated. These errors in calculating seasonal run distributions have occurred ever since the Karluk River weir began operations in 1921, and were significant during 1945–75 when the weir was located at Karluk Lake, 40 km from the ocean.

[18] See footnote 14.

Genetic Differences

Wilmot and Burger (1985) examined the genetic variation of spring- and fall-run sockeye salmon in the Karluk River during 1978–81. Spring and fall runs had significant genetic differences and were reproductively isolated subpopulations, as Thompson (1950) had predicted. The biochemical evidence did not directly dispute the idea of an originally unimodal sockeye run, but the differences in spring and fall runs were thought to be of natural origin rather than from overfishing the midseason fish.

Persistence of Productive Subpopulations

Thompson believed that Karluk's sockeye salmon had many independent subpopulations, the most plentiful originally being midseason fish. Despite several decades of effort to protect and enhance this run segment since 1950, these fish failed to increase and the run distribution has remained bimodal into present times. If midseason sockeye were originally abundant and productive, why didn't they respond to rehabilitation efforts? One reason might be that they were completely exterminated, though a fishery is seldom so efficient that abundant subpopulations are entirely harvested. River barricades, such as those used on the lower Karluk River in 1888 and part of 1889, completely blocked the sockeye migration and potentially allowed all fish to be harvested. Continued use of such river barriers would decimate all or part of a sockeye run, but these were not used at Karluk after 1889 because of federal prohibitions and rivalry between canneries. Reportedly during the early fishery, beach seines functioned as a barrier at Karluk Spit, the nets being continuously operated so sockeye salmon could not enter the river (Roppel, 1986). Yet, once the fishery moved to the ocean off Karluk Spit in 1889, fish freely entered the river at times during stormy weather and fishing closures, though harvests in the lagoon continued until 1898. Because of fishery inefficiencies it seems likely that at least some midseason sockeye, if abundant, reached the spawning grounds and should have increased in abundance when protected.

In 1952 Nelson questioned the idea that midseason sockeye were originally abundant and productive at Karluk, wondering how they could be so drastically reduced in the early fishery without spring and fall runs also being depleted. Supposedly, the spring and fall subpopulations were less productive and less able to withstand heavy fishing:

> [Concerning Karluk River sockeye salmon] The FRI through the cooperation of the Alaska Packers Association at San Francisco has obtained certain daily catch records for the early years, that is 1890 or so, until 1921. From these records they find that the major run occurred during the mid-season or during July. At that time the curve of appearance of the run according to Bevan was unimodal. It is their contention that overfishing during the mid-season has depleted the heart of the run, and now only the early and late runs are apparent. . . . As to whether the FRI is correct is problematical, but the possibility exists. It must be remembered that before the White Act in 1926 fishing occurred during the entire season. Under such conditions, how it was possible to destroy the center run without destroying the early and late runs, when according to the FRI the center run is the most prolific, is not clear to me.[19]

Thompson (1950) believed that Pacific salmon had great resilience in maintaining their populations despite intense fishing and expected midseason sockeye to respond to new regulations at Karluk (Thompson and Bevan, 1955):

> In fact, such resilience is the only explanation possible for the continuance of great runs into the Sacramento, the Columbia, the Fraser, the Karluk, and Bristol Bay despite tremendous fisheries over three-quarters of a century. This should give regulatory authorities in Alaska the courage to experiment. Every year is not a life and death crisis.
>
> Historically, the best run occurred during July and August in early days, a period now very poor. Under the theory that the period of the largest natural run is the most productive, it would be indicated that the original, but now nearly lost, runs of those two months are what need restoration, and that the earlier part of the season does not. Thus any shift in the fishing time toward the early part of the season will be desirable.

Uniqueness of Bimodality

Even though most sockeye salmon streams on Afognak and Kodiak Island have unimodal run distributions, Karluk's bimodal run is not unique to the region. Two streams entering Olga Bay on Southwest Kodiak Island, Upper Station and Akalura, have bimodal sockeye runs (Barrett and Nelson, 1994). Furthermore, bimodal sockeye runs are known from the Alaska Peninsula and Cook Inlet. Thus, Karluk's bimodal sockeye run is not an exclusive phenomenon for Kodiak Island and southwestern Alaska.

Later Doubts by Thompson?

Throughout the 1950s Thompson continued to assert that Karluk's sockeye run was originally unimodal and that commercial fishing on midseason fish changed this to bimodal. Bevan's corrections of early case-pack data were not large enough to change his conclusions.[20] In 1955 Thompson and Bevan proposed greater protection of Karluk's midseason sockeye, hoping these fish would recover to their former abundance.

Shuman and Nelson evaluated Thompson's ideas and the consequences for the FWS's research program at Karluk. Shuman rejected Thompson's thesis, citing as evidence that sockeye runs had always been bimodal as far back as cannery personnel and beach seine bosses could remember. He believed that the early case-pack data incorrectly reflected run distributions because of fish imported to Karluk's canneries. Nelson claimed that the bimodal run pattern existed at least as far back as 1912:

> [Concerning Karluk River sockeye salmon] To begin with, we find upon plotting the time of appearance of the run for each year that generally two modes are apparent. These modes usually occur in the latter part of June and the latter part of August. This condition has prevailed since 1921 and according to Mr. Axel Carlson, beach seine boss at Karluk, this has been apparent to him as far back as 1912.[21]

By 1958 Nelson questioned whether Thompson still believed in the original unimodal run pattern and midseason productivity of Karluk's sockeye:

> [Concerning Karluk River sockeye salmon, 1958] As to whether the middle portion of the Karluk run is more productive then the spring or fall runs is still questionable in my mind. Is this hypothesis still held by Dr. Thompson? I recall that he mentioned to Clint Atkinson a couple of years ago that this was one of the most serious mistakes he ever made. He did not mention the reasons for this. Possibly this might have caused some hardship to the packing industry when the Fish and Wildlife Service imposed increased restrictions to protect the center of the run or possibly he errored in the interpretation of the data.[22]

[19] Letter (21 Oct. 1952) from Philip R. Nelson, Fishery Research Biologist, Seattle, WA, to John Lutz, FWS, Kodiak, AK. Located at NARA, Anchorage, AK.

[20] See footnote 6.

[21] See footnote 19.

[22] Memo (16 April 1958) from Philip R. Nelson, Fishery Research Biologist, Annapolis, MD, to W. F. Royce, Assistant Regional Director in Charge of Research. Located at NARA, Anchorage, AK.

Nevertheless, Van Cleve and Bevan (1973) continued to affirm that Karluk's original sockeye salmon run was unimodal and had abundant midseason fish, suggesting that Thompson had not changed his conclusions.

Historical Evidence of the Seasonal Run Distribution

Because Karluk's sockeye salmon were abundant during the early fishery, knowing the original run distribution is important for research and management purposes. To gain some insight into the original run distribution of Karluk's sockeye salmon, we searched the historical fisheries literature prior to 1910 for evidence of unimodal or bimodal run patterns. Following is a chronological listing of quotations about run timing, with an assessment of whether the citation indicates a unimodal or bimodal run distribution.

1790: Merck

The naturalist Carl Heinrich Merck visited Three Saints Bay, Kodiak Island, in late June and early July 1790 as part of a Russian voyage of exploration to Alaska. Merck described in his journal, along with a later compilation of the voyage by Z. D. Titova, the seasonal movements of salmonid fishes on Kodiak Island, but did not specifically mention the Karluk River (Pierce, 1980):

> The red fish comes up the rivers from May to September, but not into every river. The white fish also come up the rivers, and the *gorbusha. Chavych* comes only at the beginning of the season, and only a few of them. People catch the fish with nets made of thin strings of sinews . . .
>
> [Speaking of the Alutiiq residents of Kodiak Island] In the month of April they move from winter to summer dwellings, which are in places rich in fish and whales . . . The first fish which they get are halibut . . . The other fish are the red, humpback, kizhuch, and the white fish (sig). They catch these fish until September . . . In October, when all fishing is ended, they return to the winter dwellings . . .

These statements give no information on unimodal or bimodal run distributions, but do convey a general idea of the salmon migrations in 1790.

1802–03: Davydov

The Russian naval officer Gavriil Ivanovich Davydov (1977) spent the winter and spring of 1802–03 studying Kodiak Island and its Alutiiq people. He mentioned Karluk in his journal as a location to stock up on dried salmon, but his notes about fishes were general comments for Alaska and eastern Russia:

> The time when the fish will appear is so well known by the inhabitants that they place as much, if not more, reliance in it than others do in the ripening of a crop. Nearly all the fish coming up the river are of the salmon species, but not every species comes up every river, and in some rivers the fish go up early and in some late. The inhabitants, in anticipation of this, block the river with a dam or fish weir. . . .
>
> [Speaking of sockeye salmon] This appears first in almost all the rivers.

His statement gives little information on salmon run distributions, except that sockeye arrived first at streams. The reference to early and late runs may refer to sockeye, but could also refer to other salmon species.

1824–25: Khlebnikov

Kiril Timofeevich Khlebnikov, an office manager for the Russian-American Company, was stationed at Sitka, Alaska, from 1818 to 1832. His duties required him to travel widely in Alaska, and in June 1825 he visited the Kodiak district to gather data on company operations and possibly visited Karluk (Khlebnikov, 1994):

> [Speaking of the Karluk River, 1824 or 1825] A stream has been discovered here which is regularly visited by enormous quantities of ocean fish every year, so with great difficulty a reliable wooden fish weir has been built. During the fish run free women are brought in to clean them and are paid for the time they work. The principal preparation is of iukola or dried fish from red and humpback salmon. The early run of fish begins in April, while the real run begins from the middle of June or the beginning of July and lasts up to October. Hence, it [the iukola] is issued to Aleuts being sent to hunt sea otters and is sent by boat or baidaras to Pavlovsk Harbor.

The cited dates refer to the Julian calendar, which in the 1800s was 12 days behind the modern calendar. Thus, mid June (Julian) = late June (modern).

It is uncertain from Khlebnikov's statement if the run pattern was unimodal or bimodal. The beginning and ending of the salmon run match present-day knowledge, but Khlebnikov was unclear whether sockeye or pink salmon composed the "real run" starting in late June or mid July. If he were speaking of sockeye salmon, this would be evidence of a unimodal pattern; if he meant pink salmon it may be evidence of a bimodal pattern. The exact year that Khlebnikov described is also unclear. He visited the Kodiak district in 1825, but the Karluk data may have come from that visit or from reports by Russian workers in 1824. This makes it impossible to conclude if the "real run" was a migration of even-year pink salmon or odd-year sockeye salmon.

1861: Golovin

Pavel N. Golovin, a Russian Naval Captain, was sent to Russian America in 1861 to investigate conditions in the Alaskan colonies. He described the existing fishing industry and discussed Russian plans to develop commercial salted-salmon operations at the Karluk River. However, his observations on salmon run distribution were general comments for the Kodiak Island area, not specifically for Karluk (Dmytryshyn and Crownhart-Vaughan, 1979):

> Fish are prepared in the colonies for the most part as food for the inhabitants; only a small amount goes abroad for sale. Seasonal fish begin to appear along the coast in March, sometimes in February, especially herring. On Kodiak they come in June and November, . . . Red fish of the salmon variety begin to appear in May; these have various names in the colonies. This fish is generally salted and dried, in which state it is known as iukola.

This gives no information on sockeye run distribution, except that it began in May.

1880: Bean

Tarleton Bean, an ichthyologist of the U.S. Commission of Fish and Fisheries, traveled north to Alaska in 1880 with William Dall, Commander of the U.S. Coast Survey schooner *Yukon*. They stopped at Kodiak on 9–14 July 1880, but did not visit the Karluk River. While in Kodiak, Bean interviewed several residents who knew about Karluk River salmon and later corresponded further with these people. In his 1887 report he described the 1880 operations of two companies that prepared salted salmon at Karluk Spit, the Western Fur and Trading Company, and Smith and Hirsch:

> [Speaking of the Karluk River sockeye salmon, 1880] In the beginning of July red salmon became scarce, and after the run of humpbacks (*O. gorbuscha*) set in (July 12), the red salmon (*O. nerka*) disappeared altogether. Smith & Hirsch stopped fishing until August 14, when the red salmon again made their appearance. . . . Red salmon are abundant every year at Karluk.

Bean clearly described a bimodal run distribution for Karluk's sockeye salmon, and his statement was powerful in being made by a trained biologist prior to large cannery harvests. The season run distribution he described in 1880 matches present-day run characteristics.

In many later publications, Bean (1889, 1890, 1891, 1894) mentioned Karluk's huge pink salmon run of 1880 and gave further information on pre-fishery sockeye runs:

> [Speaking of the 1880 pink salmon run, Karluk River] Mr. Charles Hirsch, of the Karluk Packing Company, San Francisco, has recently described to us an unusual run of this salmon in Karluk River. About the 6th of July, 1880, a glut of humpbacks came into the Karluk and continued five weeks, during which time no other salmon could enter the river. It was impossible to pull a boat across the stream.
>
> We have seen how an unexpected run of Humpbacks may prevent the Red Salmon altogether from entering its chosen river.

These statements imply a bimodal run distribution for sockeye, with a seasonal low in early or mid July. The large pink salmon run of 1880 occurred for five weeks starting in early July, just when midseason sockeye, if present, would be expected to enter the Karluk River. Bean claimed that pink salmon excluded other salmon from entering the river, but this seems unlikely for biological reasons. Salmon returning to their natal stream tenaciously pursue their spawning grounds, no matter what obstacle. If abundant midseason sockeye actually returned to the river in 1880, they would migrate upstream with the pink salmon. Since pre-fishery midseason sockeye runs, if present, should have been large in 1880, it is doubtful they would be denied access to the river. More likely, the lack of sockeye salmon in July 1880 reflected their natural midseason lull between the spring and fall runs. Run timing for the 1880 pink salmon was the same as in present times.

1889: Bean

Bean returned to Alaska in 1889 and studied Karluk's fisheries from 2 August to 7 September. Although Karluk's salmon canneries began operating in 1882, sockeye catches remained fairly small until 1888. Thus, Bean's 1889 observations at Karluk were made halfway through the second year of large harvests. His 1891 report gave the first detailed description of the commercial fishery, the sockeye salmon runs, and Karluk Lake spawning grounds:

> [Speaking of Karluk River sockeye salmon, 1889] For some reason unknown to us the salmon were late in making their appearance at Karluk in 1889. Up to the first of August the outlook for the fishermen was very discouraging, but during the month of August the arrivals of fish were numerous and the schools very large.
>
> When we left Karluk at the end of August the Red Salmon were still running into that river, but had greatly diminished in numbers and had become so dark in color as to be unfit for canning. . . . The season usually begins in June, and fish, which have not yet spawned, continue to arrive as late as the beginning of September. Spawning certainly takes place in August,

as we know from personal observation. Dead fish and others which have spawned and are already dying are very abundant about the middle of this month. We did not find many Red Salmon on our way up the Karluk River.

These descriptions of Karluk's sockeye salmon runs in 1889, very early in the commercial fishery, match the present-day bimodal pattern. Bean arrived at Karluk during the lull between the spring and fall runs, saying fishermen were disappointed, but the large fall run arrived in August and greatly increased the harvests. Upon traveling to Karluk Lake in mid August, he was surprised to see few live spawning fish, but many salmon carcasses from the large spring run littered the spawning grounds. These seasonal events are typical of present-day bimodal conditions on the spawning grounds, with a lull between the spring and fall runs.

1889: Stone

Livingston Stone, a fish culturist with the U.S. Fish Commission, traveled with Bean to Karluk in 1889 to investigate Alaska's salmon fisheries and explore the region for potential hatchery sites. After observing the commercial fishing and cannery operations at Karluk Spit in early August, Stone and Bean visited Karluk Lake for a firsthand view of the sockeye's spawning grounds (Stone, 1894):

> The Karluk River, on Kadiak Island, is probably the most wonderful salmon river in the world. On August 2, 1889, the cannery nets caught on Karluk Beach, at the mouth of the river, 153,000 salmon by actual count. A short time after, the writer went up the Karluk River in a bidarka—the skin boat of the natives—expecting to see myriads of salmon spawning and thousands on their journey to the spawning-grounds, but instead of the wonderful sight we anticipated, our whole party, I think, saw less than a dozen in the river till we reached the lower spawning-grounds, and then, to our astonishment, we saw only a few scattering fish spawning, such as one might expect to see in the most commonplace salmon river in the world; 153,000 salmon caught in one day at the mouth of the river, and none to speak of going up the river to reproduce their species. Every one can draw his own inference. The fact is significant enough.

Stone was obviously surprised by the huge commercial harvest of sockeye salmon and disappointed by the apparent paucity of spawning fish at the lake in August. From this dramatic contrast he concluded that Karluk's commercial fishery was decimating the sockeye salmon; this eventually caused him to propose a National Salmon Park on Afognak Island. However, his mid August observations of few spawning sockeye at Karluk Lake match the normal lull between the spring and fall runs.

1890: Porter

Robert Porter (1893), superintendent of the U.S. Census Office, reported on Alaska's population and resources for the Eleventh Census (1890) and included information on Karluk's sockeye salmon:

> [Concerning the Karluk River sockeye salmon, 1890] During the season of 1890, when the fishermen at Karluk were paid a bonus on each fish caught, the accounts footed up considerably over 3,000,000 fish. The season or "run" extends from June until the beginning of September, but it is interrupted at various times by "slack intervals", lasting from 1 to 2 weeks.

The slack intervals he mentioned may indicate the lull between spring and fall runs.

1896: Tingle

George Tingle (1897), U.S. Inspector of Salmon Fisheries, briefly visited Karluk in mid August 1896 on his annual inspection tour of Alaskan canneries:

> [At Karluk, mid August 1896] The business is conducted here with perfect system, more fish being at hand any day than the canneries in operation could pack. The run of fish in June did not amount to anything; indeed, the Alaska Packers Association did not pack a salmon in that month, on the spit, but July, August, and up to late in September the sea swarmed with fish. . . . From August 15 to September 1 the red salmon run was at its height. It was not unusual to haul in 25,000 to 40,000 fish.

Tingle's comments may indicate either a unimodal or bimodal run distribution. Failure of the June run suggests a unimodal pattern existed in 1896, but canneries anticipated a spring run, indicating that it normally occurred. Peak run abundance occurred from 15 August to 1 September, similar to the present-day pattern for fall-run sockeye.

1897: Moser

Jefferson Moser, US Navy Commander of the Steamer *Albatross,* investigated Alaska's salmon fisheries in 1897 for the US Fish Commission and visited Karluk's canneries on 18–20 July and 2–6 August. Fisheries expert Alvin B. Alexander of the US Fish Commission gathered most of the data at the Karluk canneries and hatchery (Moser, 1899):

> [Speaking of Karluk River sockeye salmon, 1897] . . . it will be noticed that they run first in the Karluk district,

where packing usually begins during the first days of June. . . . At Karluk the early run usually consists of fish from 14 to 15 and even as high as 17 to the case, but as the season advances they come down to 12.

The time of run is no less remarkable than the numbers of fish. The canneries count for a certainty on obtaining fish from the middle of June to the middle of September. Some years the packing has commenced the latter part of May, and again it has continued into October. Some cannerymen state that the Karluk packing season is from June 1 to September 30. . . . There are undoubtedly straggling redfish very early in all localities in Alaska, and in a place like Karluk, with a catch of nearly 2,000,000 fish, these early stragglers must come in sufficient numbers to warrant commencing cannery operations, . . . Proximity to the sea is, no doubt, also favorable to early runs. The late runs may be accounted for by similar reasoning. It is said that the fish in the late runs are in excellent condition.

Few salmon were taken at the hatchery for spawning purposes from the 20th of July to the 5th of August. . . . The cause for this remarkable scarcity of salmon at the hatchery was attributable to the frequent seine hauls made inside the mouth of the river near the canneries, from 8,000 to 10,000 being taken there daily. Fish which escaped the seines off the spit were almost certain of capture before they could get very far up the river, thereby minimizing the chances of many being secured at the hatchery. . . . It was subsequently learned that during the latter part of August a number of good hauls of salmon were made off the hatchery.

[18–20 July and 2–6 August 1897] At the time of the writer's visit to the river the daily catch of salmon was small. . . .

While Moser and Alexander's statements have some ambiguity, their observations indicate an early and late run of sockeye salmon, each run with differently sized fish. As typical of most regulatory visits to the early canneries, the inspectors arrived at Karluk during, or near to, the lull period between the early and late runs.

1898–1900: Kutchin

Howard Kutchin (1899), U.S. Special Agent for Protection of Alaska Salmon Fisheries, briefly visited Karluk in mid July and early August 1898 on his annual inspection tour of Alaska's salmon canneries:

[12 July 1898] At Karluk, where is located the most extensive plant in Alaska, the property of the Alaska Packers' Association, the season at this date was a practical failure. The spring run had not materialized, and the catch was to be counted by hundreds of cases instead of thousands as usual.

[10 August 1898] As I learned that little or nothing was doing at Karluk, there still being no run of salmon worthy of the name, it did not appear advisable to spend so much time there.

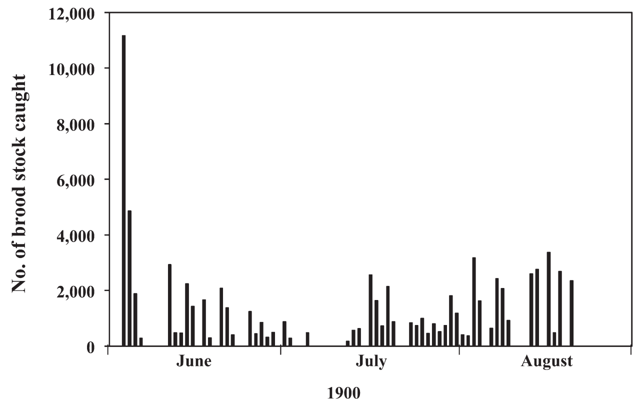

Figure 6-5. Seasonal capture of adult sockeye salmon brood stock at the Karluk Lagoon hatchery, June–August 1900 (Kutchin, 1901).

Though the early sockeye run was weak in 1898, Kutchin called it the "spring run" and indicated that it previously supplied the canneries with thousands of canned salmon cases. He arrived at Karluk during the lull between spring and fall runs.

Kutchin (1901) found similar run conditions in 1900:

[At Karluk, 13 July 1900] The run of fish up to date very light, and the prospect for a good fall run extremely poor. Had it not been for the exceptional supply of salmon at Eacolek River the Karluk pack would certainly have been a failure. . . . The spring run usually begins about June 10, and is composed of the smallest fish which is put up anywhere in Alaska. It lasts only a couple weeks. The fall run starts in about July 20 and usually continues through August.

[James A. Richardson, Superintendent, Karluk River hatchery, 9 November 1900 letter] We find the earlier eggs and the September eggs were the best, while a portion of the eggs taken during the middle part of the season were of indifferent quality.

Kutchin identified the spring and fall sockeye runs; their bimodal seasonal pattern in 1900 matched present-day run timing. Likewise, daily catches of sockeye brood stock for the Karluk hatchery from 3 June to 20 August 1900 had a bimodal pattern, with a low point in early July (Fig. 6-5).

1900: Moser

Moser again investigated Alaska's salmon fisheries in 1900 and visited Karluk's canneries and hatchery on 7–9 August. Harry Fassett of the U.S. Fish Commission inspected the Karluk Lagoon hatchery for Moser (1902):

> [Karluk River hatchery, August 1900] The period of incubation varies with the temperature of the water, of course, but it is also believed to be of less duration with eggs taken from the spring run than is the case with those of the later or fall run. That is, the eggs of the spring run of redfish seem to have a more vigorous vitality, hatching more rapidly under similar thermal conditions; . . . It would appear from the above that the eggs eye very much faster with the spring run, and that the hatching range covers a much longer period. It is also apparent that in considering the hatching of redfish at Karluk the two runs must be treated separately—the runs are so marked and the prevailing conditions so radically different.

Fassett identified the spring and fall runs and mentioned biological differences between their egg development and hatching times.

1901–02: Kutchin

Kutchin (1902, 1903) again inspected Karluk's canneries and hatchery on 1–4 August 1901 and 10 August 1902:

> [At Karluk canneries, 1–4 August 1901] Up to this time the run of salmon had been extremely light, and although Superintendent Bankoroski was not at all despondent, he admitted that the season might prove pretty nearly a failure. The season runs late here, last year closing September 11. So it was possible that the later catch would be good. Later advices informed me that this is just what occurred, and that fish swarmed along the spit in quantities that have never been known since the palmy days when Karluk was the greatest salmon fishery in the world. At the time of my visit a haul of 2,000 fish was above average, but when the great fall run set in it was reported 110,000 were taken in at one haul. The profusion was so stupendous that all the adjacent canneries at Uyak, Alitak, and Chignik eked out the scarcity at those points and made good packs.
>
> [At Karluk, 10 August 1902] Captain Bankoroski, superintendent of the Alaska Packers' Association canneries at Karluk, was so kind as to come aboard and give me the particulars of the situation at this fishery at this time. He reported that the spring run had been very light, but that the summer run, which had just begun, promised to assure a good pack. However, Karluk is always liable to have surprises in store, and the pack might be materially helped out by an unexpected large run or by the surplus from Chignik. The figures given elsewhere show that this is just what resulted.

Kutchin distinguished the spring and fall runs, though he used the term "summer run" to describe the mid August beginning of the fall run. Spring runs in both years apparently were small.

1903: Rutter

Cloudsley Rutter, U.S. Fish Commission, studied Karluk's sockeye salmon as a member of the Alaska Salmon Commission in the summer of 1903. He observed the sockeye run for four months (May–August), the longest biological study yet of these salmon at Karluk:

> [Concerning Karluk River sockeye salmon, 1903] The season of 1903 was a poor year at Karluk, . . . Apparently there was a considerable run of salmon during June, for there was certainly an enormous number reached the lake. But, although there were at least two millions reached the lake, they were not noticed at Karluk. This was probably because of the strong northeast winds that prevailed during that month, which made fishing impracticable most of the time. . . . The regular run of salmon begins at Karluk sometimes during the first of June, usually about the tenth, though there are a few stragglers much earlier. In 1903 the first specimen was taken May 11, and fishing began for the cannery June 9, but good catches were not made till about July 18 or 19. The first red salmon was seen in the upper part of the river on the 20th of May. . . . Karluk has a very long season, and salmon are usually running in paying numbers till the first of September. There are two distinct though intergrading runs, the first reaching its maximum about the last of June, the other the first of August. These were not noticed in 1903.[23]

Rutter clearly described the bimodal run distribution of Karluk's sockeye salmon and how these two runs intergraded in July. The run distribution he described for 1903 was similar to present-day patterns.

1904–05: Kutchin

Kutchin (1905, 1906) again visited Karluk's canneries and hatchery on 8 August 1904 and 31 July 1905:

> [At Karluk canneries, 8 August 1904] The season has been an extremely bad one. Scarcely any "spring" salmon ran. The first pack was made June 3. A good share of the fish packed to date were received from Alitak and Chignik Bay. It is hoped that there might be a heavy fall run, . . .
>
> [At Karluk canneries, 31 July 1905] At Karluk, likewise, the early run had been very disappointing, and up to the time of my visit to Kodiak, July 31, practically no fish had been taken. Later, however, the run was better . . .

Although the early harvests of sockeye salmon were weak in both years and might indicate a unimodal pattern, Kutchin mentioned the spring and fall runs.

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[23] See footnote 7.

1907: Marsh and Cobb

Millard Marsh, U.S. Agent of the Salmon Fisheries of Alaska, and John Cobb, USBF Assistant Agent, inspected Alaska's canneries in 1907 (Marsh and Cobb, 1908):

> [At Karluk canneries, 1907]   A very good run of fish into the lagoon early in the season soon slackened and for some time the plants were behind their packs of the previous year; but later exceptionally large runs enabled them to make up the deficiency, and to ship, as early as July 30, the first full cargo of salmon to come out of Alaska in 1907.

They described the early run, lull period, and late run of Karluk's sockeye salmon in 1907.

1910: Fassett

Harry Fassett, USBF Inspector of Fisheries in Alaska, inspected the Karluk River hatchery on 1–8 September 1910:

> [At Karluk River hatchery, 1–8 September 1910]   The red-salmon eggs at Karluk are reported to be very variable in size, and a big difference is said to be noted between those of the early, or "spring", run and those of the later, or "fall", run. The fall fish are themselves larger, and have larger eggs, the eggs are more regular in size, and are in greater number. The superintendent said his average through the year is a little less than 3,000 eggs per fish.[24]

Fassett described Karluk's spring and fall sockeye runs and mentioned significant biological differences between the two, characteristics that continue to present times.

In conclusion, although some historical records of Karluk's sockeye salmon runs were ambiguous or possibly indicated a unimodal distribution, most reports described a seasonal bimodal pattern (Table 6-1). Historical records of distinct unimodal distributions and abundant midseason fish were lacking. Observations made before Karluk's commercial fishery began in 1882, or shortly thereafter (1887–95), provide stronger evidence of the original run pattern than those made in 1895–1910. By 1895 Karluk's sockeye salmon run already had sustained 8–9 years of intense commercial fishing, and later observations may reflect these heavy harvests. Thus, Bean's observations of a bimodal run pattern in 1880 and 1889 are particularly noteworthy.

[24] Fassett, H. C. 1910. Report on the salmon hatchery operated by the Alaska Packers Association on Karluk Lagoon, Kadiak Island, Alaska. Unpubl. report. 25 p. Located at Alaska Historical Collections, Alaska State Library, Juneau.

Table 6-1
Historical records of seasonal run distribution for Karluk River sockeye salmon.

Year	Source	Unimodal or bimodal distribution
1790	Merck	No information
1802–03	Davydov	No information
1824–25	Klebnikov	Possibly either
1861	Golovin	No information
1880	Bean	Bimodal
1889	Bean	Bimodal
1889	Stone	Bimodal
1890	Porter	Possibly bimodal
1896	Tingle	Possibly either
1897	Moser	Bimodal
1898–1900	Kutchin	Bimodal
1900	Moser	Bimodal
1901–02	Kutchin	Bimodal
1903	Rutter	Bimodal
1904–05	Kutchin	Bimodal
1907	Marsh and Cobb	Bimodal
1910	Fassett	Bimodal

Conclusions

Thompson's idea that commercial fishing altered the original run distribution of Karluk River sockeye salmon from unimodal to bimodal deserves serious consideration, but valid questions remain about his assumptions and conclusions. In particular, significant weaknesses exist in using historic case-pack data to predict seasonal run distributions. In fact, later corrections of the case-pack data made run bimodality more apparent in the early years, even though many midseason (July–August) sockeye were still present.

We believe that most evidence shows that Karluk River sockeye salmon originally had a bimodal run distribution (Table 6-1). Historical observations of sockeye runs prior to commercial fishing support this view. While intense commercial fishing may alter the run distributions of salmon, it seems unlikely that the bimodal run pattern that has existed for at least 130 years (1880–2010) would continue unless it was a natural biological feature of Karluk's sockeye salmon. If midseason subpopulations once bore the brunt of intense fishing and were heavily depleted, this run segment should have responded at some time to the different fishery regulations implemented.

Ever since the Karluk River weir began operating in 1921, errors in estimating the travel time of sockeye salmon between the fishery and weir have caused midseason escapements to be underestimated and later escapements to be overestimated, incorrectly enhancing reported run bimodality. Some midseason fish thought to be depleted by the fishery were actually

present in later weir counts. Run bimodality increases in the Karluk River because spring- and fall-run sockeye have different travel times to Karluk Lake, the speed being affected by river flow and pink salmon abundance. Spring-run sockeye rapidly ascend the river, while fall-run sockeye have longer travel times, a fact not always appreciated. Because travel times between the fishery and weir vary seasonally, escapement and weir count distributions differ.

One of Thompson's main contributions to understanding the seasonal run distribution of Karluk's sockeye salmon was his emphasis on the many independent subpopulations present, this biological diversity allowing these salmon to survive varying environmental and fishing conditions. His focus on Karluk's sockeye subpopulations stimulated research on this topic for many years, until their existence was documented.

CHAPTER 7

Limnology and Fertilization of Karluk Lake

From one generation to the next—a remarkable inheritance

Biologists have known for about 100 years that sockeye salmon differ from all other Pacific salmon species in homing to river systems that flow from a lake. The first two researchers to visit Karluk Lake and study its sockeye salmon in 1889 and 1903 commented upon this unusual environmental requirement, but neither understood the lake's importance as a multi-year rearing habitat for juvenile fish. Because little was then known about the life of sockeye salmon, Karluk Lake's limnology (scientific study of the physical, chemical, and biological features of lakes and streams) received scant attention; the main reason to visit the lake in the early years was to survey its salmon spawning habitats. As the freshwater life history of sockeye salmon became better known, biologists began to appreciate that environmental conditions in the nursery lake might well determine the growth and survival of its young fish and the subsequent production of smolts and adults. This insight eventually led to regular limnological sampling of Karluk Lake, and the data collected became ever more detailed and sophisticated with time.

In this chapter, we review the historical development of limnological studies at Karluk Lake from 1889 to 2010 and discuss how knowledge of the lake environment gave important information about past and present sockeye salmon production.

The Karluk Lake and River Ecosystem

Karluk Lake, the largest lake on Kodiak Island (Figs. 1-1, 1-4), was formed between two mountain ranges thousands of years ago by the scouring action and moraine deposits of glaciers. The lake is oriented in a north–south direction and contains three distinct internal basins—the large deep O'Malley basin (south end of lake), the shallower Thumb basin (middle), and the main basin (north) (Gilbert and Rich, 1927; Juday et al., 1932). Physically, Karluk Lake has a surface area of 39.5 km^2, maximum depth of 126 m, and mean depth of 48.6 m (Table 7-1). It is 19.6 km long, 3.1 km wide (maximum), and 112 m above sea level.

Because steep mountains border the lake, the shallow littoral zone and rooted aquatic plants are limited. Boulders and cobbles compose much of the lake's shoreline, but gravel and pebble substrates exist near inflowing tributaries and along some beaches. Deep-water sediments are accumulations of fine planktonic particles, especially the silica valves of diatom algae

Karluk Lake at Camp Island, looking toward Thumb basin and lake (center, in distance), June 1958. (Auke Bay Laboratory, Auke Bay, AK)

Table 7-1
Lake and river physical dimensions.[1]

	Basin location	Elevation (m)	Length (km)	Maximum width (km)	Surface area (km^2)	Volume ($m^3 \times 10^6$)	Euphotic volume ($m^3 \times 10^6$)	Littoral area (km^2)	Mean depth (m)	Maximum depth (m)	Water residence time (years)	Drainage basin area (km^2)	Light compensation depth (m)
Karluk Lake		112	19.6	3.1	39.5 (100%)	1920 (100%)	780 (41%)	7.6 (100%)	48.6	126	4.8	282	23
Main Basin	north				15.1 (38%)	471 (25%)		4.2 (55%)	31		3.7		25
Thumb Basin	center				4.3 (11%)	116 (6%)		1.3 (17%)	27		1.3		23
O'Malley Basin	south				20.1 (51%)	1333 (69%)		2.1 (28%)	66		7.1		21
Thumb Lake		113	1.1	0.7	1.1	2.9				9.8	13 days		
O'Malley Lake			3.4	0.4	2.2								

	Length		Width		Water depth	Discharge		Gradient	Total drainage area	Mean annual precipitation
	(km)	(miles)	(m)	(feet)	(m)	Mean (m^3/s)	Range (m^3/s)	(%)	(km^2)	(cm)
Karluk River	39.9	24.8	18–165	60–540	0.3–3.0	12	2–50	0.28	620	172
River Mouth to Upper Lagoon	5.0	3.1								
Upper Lagoon to Lower Weir	0.2	0.1								
Lower Weir to Portage	19.8	12.3								
Portage to Lake Outlet	14.2	8.8								
River Mouth to Lake Outlet	39.9	24.8								

[1] Lake values from Koenings and Burkett, 1987b.

that have accrued for thousands of years. Several hundred taxa of diatoms and green algae account for most of the lake's phytoplankton, while the macrozooplankton community is primarily made up of five taxa, *Bosmina longirostris, Daphnia longiremis, Cyclops columbianus, Diaptomus pribilofensis,* and *Epischura nevadensis* (Juday et al., 1932; Hilliard, 1959a; Manguin, 1960; Terrell, 1987; Koenings and Burkett, 1987b; Kociolek and de Reviers, 1996; Gregory-Eaves et al., 2003; Sweetman and Finney, 2003).

Karluk Lake is clear, cool, and oligotrophic. Maximum water temperatures in summer seldom exceed 15°C at the surface (Fig. 7-1); the lake usually accumulates its seasonal maximum heat content (calories/cm^2) between 25 July and 16 August (Koenings and Burkett, 1987b). Water transparencies are typically 5–10 m and the mean light compensation depth is 23 m. Surface waters have mean concentrations of total phosphorus of 5.5–9.3 μg/L and chlorophyll-a of 0.9–3.3 μg/L (Schrof et al., 2000). Karluk Lake has a drainage basin area of 282 km^2, an average annual precipitation of 172 cm, and a water residence time of 4.8 years. The lake's surface area covers a significant portion (14%) of its drainage basin (Fig. 1-5), an important factor that affects the quantities of mineral nutrients coming from inorganic watershed sources. The lake is usually ice-covered in December–April (sometimes May), but it remains ice-free in rare mild winters (e.g. 1925–26, 1957–58). An unusual phenomenon occasionally occurs during spring breakup, when brisk winds push lake ice onto the shoreline; momentum crumbles the crystal matrix and builds an ice ridge that pushes a short distance inland (Atwell, 1975).

Two types of tributary streams enter Karluk Lake—lateral and terminal. Lateral tributaries are relatively small streams that rapidly descend steep mountain slopes and typically have waterfalls or cascades that limit the upstream migration of salmon. About 12 lateral streams enter Karluk Lake: (clockwise from outlet) Spring, Moraine, Cottonwood, Bear (sometimes identified as two small creeks, Little and Big Bear), Alder, Little Lagoon, Cascade, Meadow, Eagle, Halfway, and Grassy Point creeks (Fig. 1-5, Table 7-2). Salmon Creek, also classed as a lateral stream, joins the Lower Thumb River

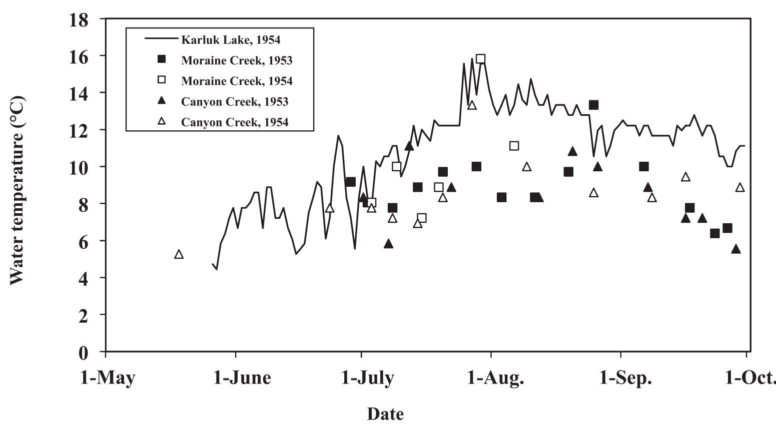
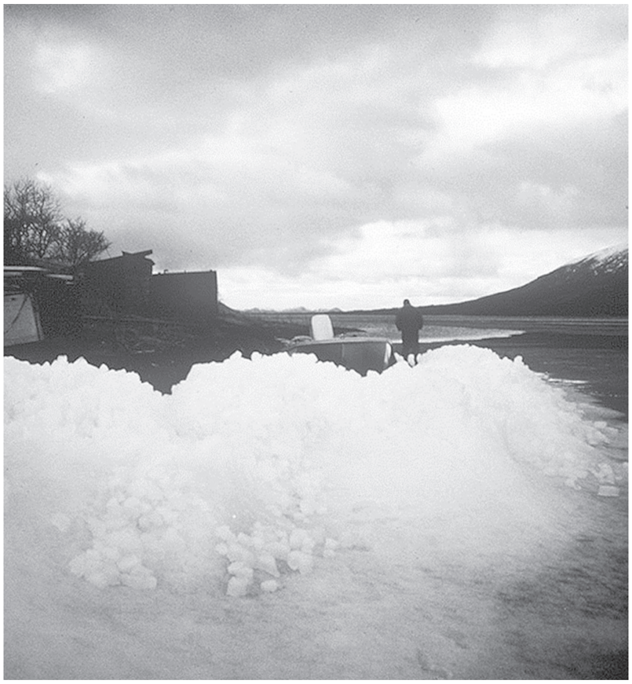


Figure 7-1. Surface water temperatures of Karluk Lake (1954), a lateral tributary (Moraine Creek, 1953–1954), and a terminal tributary (Canyon Creek 1953–1954). From Bevan and Walker (1954, 1955).

Karluk Lake ice cover, looking toward Thumb Lake and valley, spring 1969. (Benson Drucker, Reston, VA)



Shoreline ice ridges, Camp Island, Karluk Lake, spring 1968. (Benson Drucker, Reston, VA)

O'Malley Lake, tributary to the south end of Karluk Lake, September 1952. (Charles E. Walker, Sechelt, BC)

just below Thumb Lake. Falls Creek, another lateral stream, flows into the upper O'Malley River. A few small unnamed lateral streams also exist, but they only have enough water for salmon spawning in wet years.

Two main terminal tributaries enter Karluk Lake from broad valleys, the Thumb and O'Malley rivers; both are somewhat larger than the lateral streams and have their own small lakes. The Lower Thumb River flows 0.8 km from Thumb Lake (1.1 km^2) into Karluk Lake. Upstream of Thumb Lake, the Upper Thumb River divides into its North and East Forks. The O'Malley River flows 0.8 km between O'Malley Lake (2.2 km^2) and Karluk Lake, with Canyon Creek, often considered a third terminal tributary, joining this river just upstream of Karluk Lake. Originally, Canyon Creek flowed directly into Karluk Lake, but the creek channel shifted to enter the lower O'Malley River in 1928. Likewise, the route of Falls Creek has changed over the years. For many years, Falls Creek discharged into the upper O'Malley River, but a storm in September 1947 eroded a new channel that entered the north end of O'Malley Lake. ADF biologist Clint Stockley diverted the creek back to its original channel in 1953, but another storm in August 1954 shifted it again to the lake (Bevan and Walker, 1955).[1] Recent maps show that Falls

Table 7-2
Karluk Lake and River tributary streams.

	Tributary length[1] (km)	Salmon migration barrier	Distance to barrier (km)
Karluk Lake			
Spring Creek	0.8	none	
Moraine Creek	6.3	cascades	2.4
Cottonwood Creek	4.3	4 m falls	1.0
Bear Creek	1.3	none	
Alder Creek	2.9	falls	
Little Lagoon Creek	0.3	cascades	
Lower Thumb River	0.8	none	
Upper Thumb River	0.6	none	
North Fork Upper Thumb River	5.8	15 m falls	2.5
East Fork Upper Thumb River	12.9	2.5 m falls	3.0
Salmon Creek	5.6	2.5 m falls	0.8
Canyon Creek	9.7	2.5 m falls	1.6
Falls Creek	6.9	11 m falls	2.4
O'Malley River	0.8	none	
Cascade Creek	4.5	cascades	1.1
Meadow Creek	3.9	1.5 m falls	
Eagle Creek	2.6		
Halfway Creek	3.9	falls	0.3
Grassy Point Creek	3.2	falls	0.8
Karluk River			
Silver Salmon Creek	22.5		

[1] Tributary length measured from USGS topographic maps.
"Salmon migration barrier" and "distance to barrier" measurements are less accurate because they are estimates recorded in field notebooks.

[1] Lindsley, Roy R. 1953. Annual report, Kodiak area, 1953. FWS, Branch of Alaska Fisheries. Unpubl. report. 24 p. Located at NARA, Anchorage, AK.

Thumb Lake (upper left), connected by Lower Thumb River to Karluk Lake (right), ca. 1952. (Charles E. Walker, Sechelt, BC)

Creek enters the upper O'Malley River. During the sockeye spawning season, water temperatures in lateral and terminal tributaries typically range between 6°C and 12°C, these values being about 4C° cooler than the surface waters of Karluk Lake in mid summer (Fig. 7-1).

Thumb and O'Malley lakes are shallow and similarly-sized, but differ in the amount of salmon spawning area lying upstream. Tributaries of Thumb Lake are major spawning areas for thousands of sockeye salmon, while O'Malley Lake has few spawning tributaries except for Falls Creek. This difference in upstream spawning area is an important factor controlling the productivity and limnology of these two small lakes. Water transparencies typically are 2–3 m in Thumb Lake and 4–6 m in O'Malley Lake in mid summer (Juday et al., 1932).

The Karluk River, which originates at the north end of Karluk Lake, flows 40 km north and west until it finally discharges into Shelikof Strait at Karluk Spit. In its upper reaches the river passes through a broad valley, but upon turning westward it flows through mountainous terrain and enters Karluk Lagoon 5 km east of its ocean mouth. Karluk Lagoon, a shallow estuary, fluctuates a few meters in depth with the ocean tides. The Karluk River has a mean discharge of 12 m^3/sec (range, 2–50 m^3/sec) and a bimodal pattern of seasonal flow (Fig. 7-2).[2] The first discharge peak occurs in June from snowmelt runoff; the second peak usually occurs in October–November from rainfall runoff. River flows typically decrease during summer and winter. A number of tributaries enter the Karluk River; the largest in the upper section is Silver Salmon Creek. Just downstream from the Portage, a west bank tributary that drains a small lake to the west of Barnaby Ridge enters the river.[3] River water temperatures are usually less than 15°C in summer (Fig. 7-3). Temperatures of the upper river are moderated by surface water inflows from Karluk Lake, while those of the lower river are affected by the prevailing climate and experience rapid cooling in September–October.

1889–1922: Preliminary Limnological Observations of Karluk Lake

In 1805 Urey F. Lisiansky, Captain of the Russian naval ship *Neva*, prepared the first map of Kodiak Island that showed Karluk Lake and River (Lisiansky, 1814). Over the next 50 years, other explorers published maps of the region that illustrated the approximate location of Karluk Lake and River, but they often incorrectly drew the lake's outline, suggesting that their information came from general descriptions of the area, not from precise surveys.

Bean (1891) made the first limnological observations at Karluk Lake on 17–21 August 1889, describing its physical features, shoreline substrates, tributary

[2] The bimodal flow pattern of the Karluk River has been documented for many years by the weir tenders, who daily recorded the river levels each field season (May–October). These data are recorded in the weir station notebooks at NARA, Anchorage, AK.

[3] This small unnamed lake was unofficially called Barnaby Lake by several fishery biologist in the 1930–50s, or Pinguicula Lake in the 1960s (Karlstrom et al., 1969).

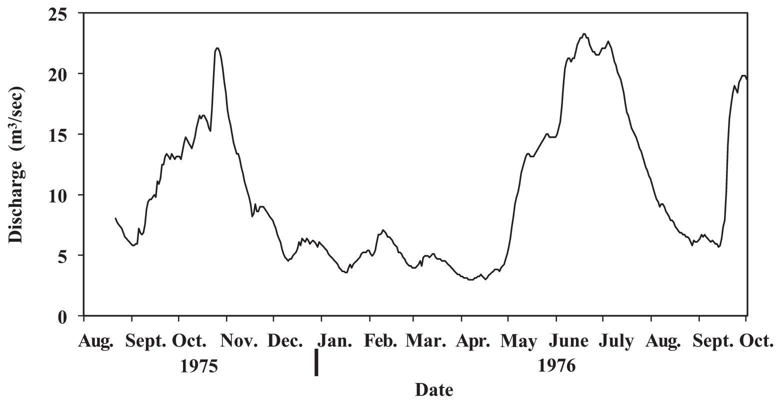


Figure 7-2. Water discharge (m^3/sec) of the upper Karluk River near the lake's outlet, 1975–76. Water survey data from U.S. Geological Survey (1974–82).

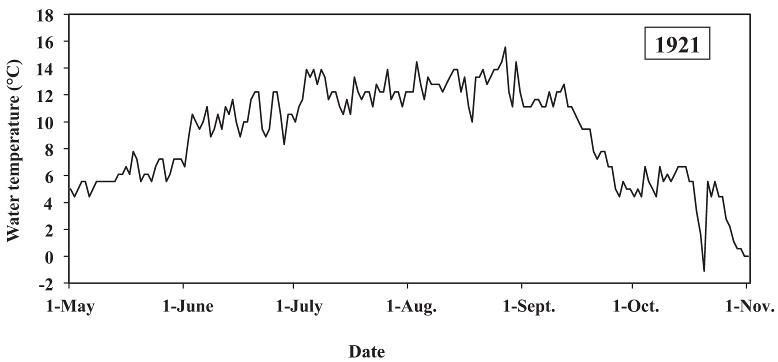
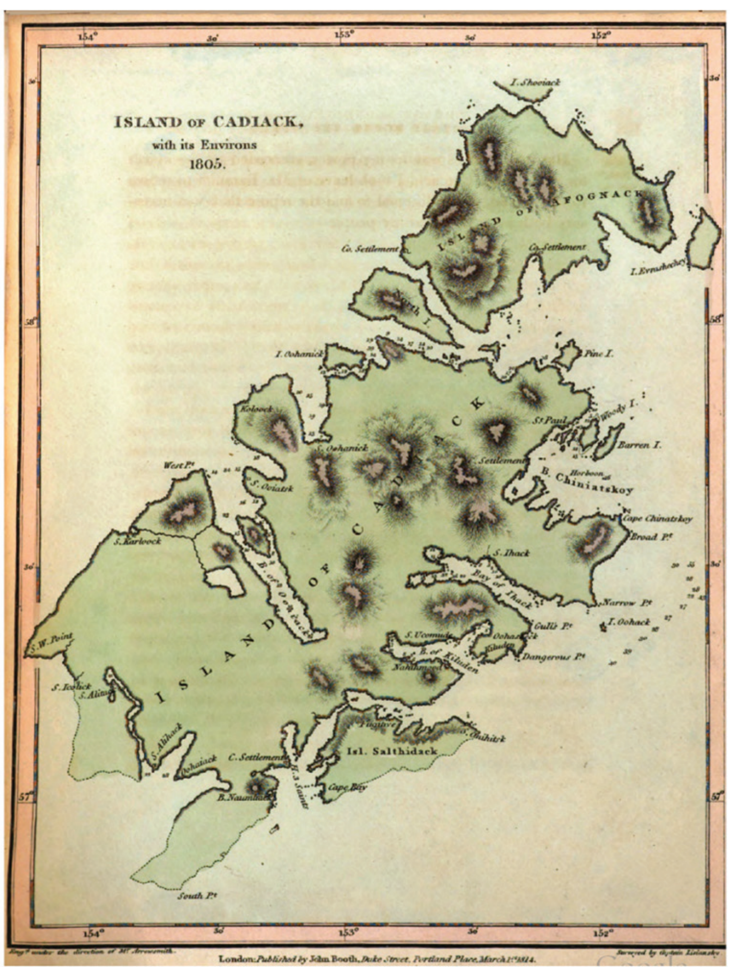


Figure 7-3. Water temperatures at the Karluk River weir, 1921. Temperature was measured at noon each day at the weir on the lower river near upper Karluk Lagoon. Unpublished USBF data from NARA, Anchorage, AK.



Early map of Kodiak Island showing Karluk Lake and River, 1805. (From Lisiansky, 1814)

streams, two tributary lakes, and surface water temperatures (9.2–12.8°C). Most of the lake's shoreline lacked aquatic plant beds, but dense vegetation occurred in some sections of the Karluk River. While circumnavigating the lake, Bean noted that the lake's "shores are covered with a greasy deposit, doubtless composed of decayed animal matter," undoubtedly the residue of past salmon carcasses. His surveyor gathered topographic data and prepared a reasonably accurate map of Karluk Lake, the tributary lakes and streams, and upper Karluk River. Bean (1891) published this first detailed map of Karluk Lake, though it was incorrectly shown as being only 13 km long. He attempted to measure the lake's depth in the upper basin about 460 m west of Island Point, but the 49 m sounding line failed to reach bottom. Livingston Stone, another member of Bean's field party, measured the water temperatures of the Karluk River (range, 9.2–15.6°C) near Karluk Spit on 4 August–5 September.

Rutter (1903a) briefly visited Karluk Lake in June 1897 and noted that "the shore of the lake for miles was lined with the bones of the salmon that had died 6 to 8 months previously." Although Rutter and his assistant spent much time at Karluk Lake in the summer of 1903, they apparently failed to collect limnological data, except for water temperatures at several locations (Chamberlain, 1907).[4] Rutter failed to grasp the importance of Karluk Lake as a multi-year nursery site for its juvenile sockeye salmon.

The APA prepared a reconnaissance survey map of the terrain between Larsen Bay and Karluk Lake in September 1906, possibly with the idea of moving the Karluk Lagoon hatchery to the lake.[5] In the process, they made 12 depth soundings (2.7–69.5 m) in the north basin of Karluk Lake. Their map showed a profile of elevations between Larsen Bay and Karluk Lake, notes on the marsh and land vegetation, tributaries of the upper Karluk River and north end of Karluk Lake, Karluk Lake depths, and Rutter's 1903 campsite, lake-outlet fish trap, and study sites of salmon spawning baskets.

Frederic Chamberlain first described in 1907 the unique life history of sockeye salmon, showing that juveniles reared for at least a year in a freshwater lake before migrating to the ocean. He learned this from his 1903–04 field studies at the Naha River, Revillagigedo Island, southeastern Alaska, and from Rutter's 1903 field work at Karluk Lake. After Chamberlain discovered this crucial life history requirement, biologists realized that the environment of the nursery lake may affect the growth and survival of young salmon. Consequently, the need to understand this freshwater habitat and collect limnological data became increasingly obvious. This biological insight, reinforced somewhat later by the unexpected discovery that Karluk's sockeye salmon had high rates of survival in the ocean, focused new research in the 1920s on the environment of Karluk Lake and the reasons for the high mortality of early life stages in freshwater.

Gilbert and O'Malley briefly visited the north end of Karluk Lake on 25–26 July 1919 and noted the rocky

Spring Creek, salmon spawning tributary at the north end of Karluk Lake, ca. 1952. (Charles E. Walker, Sechelt, BC)

[4] Rutter divided his 1903 field season between Karluk Lake and Karluk Spit, while Spaulding, his assistant, apparently spent most of the summer at the lake. Spaulding's 1903 field notebook may record limnological data, but its location is unknown. Letter (19 July 1903) from Spaulding, Karluk Lake, to Rutter [at Karluk Spit]. Located in Box 130, Barton Warren Evermann papers, Library Special Collections, California Academy of Sciences, San Francisco, CA.

[5] APA 1906 reconnaissance map located at Alaska State Library, Historical Collection, Juneau, AK and a copy at NARA, Anchorage, AK.

substrates along the west shore and gravel substrates along the east shore. Most likely, Gilbert measured the water temperatures of the lake and several tributaries. They viewed Spring Creek and claimed it remained ice-free all winter. Revisiting Karluk Lake on 8–12 August 1921, they completed their reconnaissance of its salmon spawning streams and Gilbert again described the lake and stream substrates and measured surface water temperatures. He also made several depth soundings in Karluk Lake off Tent Point, Tree Point, Eagle Point, and Long Point, finding that some depths exceeded 120 m. Gilbert returned to Karluk Lake on 18–24 August 1922 with Rich to survey the spawning salmon and again noted its water temperatures and substrates. During this visit, Rich prepared a preliminary map of Karluk Lake by measuring baselines and taking compass bearings to prominent landmarks.

1926: Willis Rich and the Origin of Karluk Lake Limnological Sampling

Willis Rich, then USBF leader of sockeye salmon research at Karluk, spent about 40 days at the lake in 1926 observing the salmon at their spawning habitats and exploring tributaries upstream to natural barriers of fish migration.[6] Significantly, in 1926 he witnessed one of the largest sockeye salmon escapements ever at Karluk, as 2,500,000 fish flooded onto the spawning grounds from a total run of over 4,500,000. This phenomenal abundance profoundly affected his understanding of the Karluk system and sparked a new limnological idea, that nutrients leached from decomposing salmon carcasses may enhance the productivity of young sockeye in Karluk Lake. Thus, Rich's work in 1926 was important in the limnological history of Karluk Lake for two reasons: 1) it marked the origin of regular sampling of physical, chemical, and biological factors at the lake, and 2) it introduced the idea that salmon-carcass nutrients may affect the lake's ability to produce sockeye salmon.

1) Limnological Sampling

Rich began the first limnological sampling at Karluk Lake in 1926. During the first two weeks of August, he prepared an accurate bathymetric map of the lake using a sextant, plane table, sounding line, and aneroid barometer. The map was useful for his future limnological studies, giving basic data on lake morphology and, for the first time, showing that Karluk Lake had three internal basins. He also surveyed Thumb and O'Malley lakes and found both to be quite shallow. Gilbert and Rich first published this bathymetric map of Karluk Lake in 1927; it continues to be useful for current limnologists and fishery biologists.

Because of Rich's many projects and ambitious plans for the 1926 field season in Alaska, he delayed the limnological sampling of Karluk Lake until mid August. Using a reversing thermometer, he measured water temperature profiles in each the lake's three basins and in Thumb Lake. He also collected many spot water temperatures wherever he traveled throughout the basin, including from surface waters of Karluk Lake in littoral and limnetic zones, tributary creeks, lagoons, and rivers, seepage zones, Karluk River, and nearby tundra ponds. In addition, the USBF weir tenders at the Portage monitored daily river temperatures from 29 May to 6 September.[7] To measure water transparencies, Rich used an improvised enamelware dinner plate as a Secchi disk and found the values to be relatively high in Karluk Lake, low in Thumb Lake, and intermediate in O'Malley Lake. He collected plankton from all three lakes by towing #12 and #16 plankton nets for 5 or 10 minutes, but distrusted his gear to correctly sample from specific lake depths and proposed using a hose and pump in future years. Upon returning to Larsen Bay on 5 September, he examined the plankton samples and found them "very interesting, but we obviously need to have more exact quantitative data and much more exact data as to the depth at which the sample was taken." Thumb Lake had much higher plankton densities than did Karluk or O'Malley lakes. Rich also collected bottom sediments for diatom analysis by Albert Mann of the Carnegie Institute of Washington, but the improvised sampling device, made from a metal can and fishing weights, often failed to retrieve the fine sediment. No water chemistry measurements were made in 1926.

In spite of Rich's plans to study Karluk Lake in 1926, most of his limnological work that year was devoted to field testing the sampling gear. First, he spent only two weeks in August actually collecting the limno-

[6] Rich, Willis H. 1926 notebook. He was at Karluk Lake on 27–28 June, 12–22 July, and 29 July–27 August 1926. The location of his original notebooks are unknown, but copies were located at NARA, Anchorage, AK, and ABL Library, Auke Bay, AK. Also see Rich (1963).

[7] Hungerford, Howard H. 1926. Report of operations at Upper Karluk Weir, season of 1926. Department of Commerce, USBF. Unpubl. report. 5 p. Located at NARA, Anchorage, AK.

logical data because his many other projects had already absorbed much of the field season. Second, his Secchi disk and bottom sediment sampler were improvised devices and his plankton nets had problems. Consequently, Rich lacked confidence in the 1926 data and most of these were never published, except for one water temperature profile (Juday et al., 1932). Nevertheless, the 1926 limnological studies led to a more complete and accurate program in 1927. The first limnological publication on Karluk Lake was a short note by Rich and the renowned limnologist, Edward A. Birge of the University of Wisconsin, based on water temperatures collected by Rich in 1926 (Birge and Rich, 1927).

Associated with his limnological studies of Karluk Lake, Rich keenly observed a wide variety of the lake's flora and fauna. He noted that few aquatic plants grew along the narrow rocky shorelines of Karluk Lake, but dense plant beds occurred along gentle-sloping beaches, in the shallow waters of Thumb and O'Malley lakes, in the quiet reaches of some tributaries or bays, and in the slow-flowing Karluk River near the Portage. On a trip upriver from the Portage on 12 July 1926, he noted "the large bright green, feathery cresses of the crowfoot are very beautiful and are now in bloom."[8] He collected and identified some of the common species of aquatic plants in the Karluk ecosystem, including the water buttercup, *Ranunculus aquatilis;* two species of pondweed, *Potamogeton;* horsetail, *Equisetum;* and pond lily, *Nuphar.* In subsequent field seasons he collected additional aquatic plant species and confirmed previous identifications by searching out the diagnostic flowers and fruits.

Besides these botanical observations, Rich also searched for and collected various aquatic macroinvertebrates in their natural habitats at Karluk Lake, one of few fishery biologists to ever check these benthic animals. He occasionally looked under shoreline stones at Camp Island and found leeches, hydroids (*Hydra*), and a flatworm with green symbiotic algae. Digging into sockeye salmon redds to examine the eggs, he found many aquatic oligochaete worms. On a trip to O'Malley Lake on 16 August 1926, he saw freshwater mussels embedded in the substrate (he called them *Margaritana margaritifera*) and aquatic snails gliding over the sediments (*Planorbis* and *Lymnaea*).[9] Furthermore, the bottom sediments of Karluk Lake contained unique silicon spicules that documented the presence of freshwater sponges (Juday et al., 1932).

2) Origin of the Sockeye Salmon Carcass Nutrient Idea

The idea that nutrients leached from adult salmon carcasses may influence the productivity of Karluk Lake originated with Rich and the huge run of sockeye in 1926. This cornucopia of fish exceeded all previous runs seen by biologists at Karluk and possibly equaled the magnificent runs of the early fishery years. Fortunately, Rich was then present at Karluk Lake to watch the sockeye salmon fill the spawning grounds, soon followed by huge masses of decaying carcasses.

It was obvious early in the field season that the number of returning sockeye would be enormous at Karluk in 1926. As Rich worked at the counting weir in early June, he watched the masses of spring-run sockeye moving upstream, noting that "this big run of adult fish which is passing the weir now is apparently one of the best on record. It was certainly an imposing sight to see them coming on up stream in large shoals, splashing over the shallow riffles in almost solid masses."[10] A month later as he traveled around Karluk Lake, he was astounded by the hordes of sockeye salmon crowding into every available spawning habitat. Compared with his 1922 visit, the 1926 escapement was noticeably larger:

[8] See footnote 6. His field notebooks contain sketches of the aquatic plants he observed. Apparently, his Karluk plant collection was deposited in the Dudley Herbarium, Stanford University, which in 1976 was transferred to the California Academy of Sciences, San Francisco, CA. A list of plants collected at Karluk Lake by Willis H. Rich is present at the Earth Sciences Library and Map Collection [Branner], Stanford University (G4372.K28 1926.R5).

[9] Rich tentatively identified the O'Malley Lake freshwater mussels in 1926 as *Margaritana margaritifera,* there being hundreds or thousands of juveniles concentrated in substrate patches of 20–60 cm diameter (See footnote 6). He collected and preserved juvenile and adult specimens, though it is unknown if these were deposited in a museum. Years later, Morton reported seeing a freshwater mussel floating down the O'Malley River on 25 August 1941 (William M. Morton 1941 notebook located in the personal papers of Robert S. Morton, Portland, OR) and Freeman reported seeing a live clam in O'Malley Lake on 21 November 1948 (Arthur Freeman 1948 notebook located in the personal papers of Arthur Freeman, Indianapolis, IN). Freshwater mussels that once were called *Margaritana margaritifera* in western North America are now known as *Margaritifera falcata,* this species currently being unknown from Kodiak Island (Smith, 2001), though another freshwater mussel, *Anodonta beringiana,* has been collected there. In order to complete their life cycle, these freshwater mussels must have nearby host fish that are temporarily parasitized by the mussel's glochidia larvae life stage. The true identity of the O'Malley Lake mussels remains unclear.

[10] See footnote 6.

Sockeye salmon carcasses, Karluk Lake tributary, ca. 1934. (Joseph Thomas Barnaby, from Lynn L. Gabriel, Herndon, VA)

> [Thumb River & Salmon Creek, 14 July 1926] Apparently every available spawning space was occupied in the River and in the Creek. They were many times more abundant than when we were here in 1922. Just outside the mouth of Salmon Creek the fish were in the densest school I have ever seen . . . There must have been 4,000 or 5,000 fish in this one place. Immediately above the mouth of the creek they were so thick that only their noses showed—they were packed in vertically and the whole surface showed only a mass of noses sticking up above the surface. Fish were wriggling up over the top of the mass and trying to get into the stream and a continual procession of fish were entering the creek.
>
> [Upper Thumb River, 18 July 1926] Nowhere have I seen fish more abundant [or] a spawning area more thickly populated. The gravel of the river bed was everywhere crowded with spawning beds. There was apparently not a square yard of the whole river bed, wherever there was suitable gravel, that did not enter a spawning bed. . . . Almost everywhere in both branches the live salmon were in rank after rank across the streams and one rank right behind another. There are tens of thousands of dead salmon strewing the banks and gravel bars. Estimated 100,000 dead and alive between Thumb Lake and the point where the main river forks with another 100,000 in each of the 2 branches to figure up as we went . . . If anything, though, the estimate is low, and I believe that a good half million fish have or will spawn in these streams.[11]

As spring-run sockeye finished their spawning in July, salmon carcasses rapidly increased in abundance. By early August few sockeye still spawned, but decomposing carcasses littered the tributaries and lake shorelines. Rich noted abundant carcasses everywhere and the speed of their decay:

> [Thumb River, 3 August 1926] Thumb River, where it enters the Thumb, is quite a different looking stream now as compared with two weeks ago. Comparatively few live fish were to be seen, though the shore on both sides of the mouth of the river was covered with carcasses in advanced stages of decay . . . Many dead salmon are to be seen all along the shores even though there may not be a spawning region for a mile or so.
>
> [South end of Karluk Lake, 4 August 1926] Comparatively few live salmon anywhere, even in Falls Creek and O'Malley River, but dead carcasses line the shore at the head of the lake and are to be seen along all of the shores even those most remote from any spawning streams. Along the shores of Camp Island there are dead salmon averaging about one every 10 feet and sometimes more abundant than that.
>
> [North end of Karluk Lake, 5 August 1926] Live salmon scarce as usual but lots of dead ones. The shore all along the foot of the lake, from Spring Creek to the outlet, is thickly covered with the old decayed remains of spawned out salmon and with the skin and bones left after the myriads of blow flies have done their allotted task.
>
> [O'Malley River, 8 August 1926] . . . the vast majority of the tremendous numbers we saw three weeks or so ago are now dead and their carcasses are rapidly disintegrating and will soon have entirely disappeared. I am impressed by the speed with which this disintegration takes place . . .
>
> [Cascade & Meadow creeks, 8 August 1926] . . . multitudes of dead salmon piled up in great masses against the larger boulders, lining the banks and rapidly disintegrating under the influence of decay and blow flies.
>
> [Upper Thumb River, 9 August 1926] There are only a few thousand live fish left in the whole system, most of the multitudes we saw spawning at the time of our previous visit being dead and nearly rotted away. [Thumb River] bed with the thousands of rotten carcasses piled

[11] See footnote 6.

up against every boulder and in each gravel bar and the dried skins and bones left on the exposed portions of the bars and banks was a sight to behold.[12]

Significantly, in early August Rich observed a dense phytoplankton bloom in Thumb Lake and linked it to the nearby decaying salmon carcasses:

[Thumb Lake, 9 August 1926] Thumb Lake was a marvelous site as the water was colored a brilliant green by some minute cellular green alga. The transparency was very low as whitened dead fish could hardly be seen at a depth of 4 or 5 feet. The oars dripped emeralds and along the shore the frothy bubbles were as green as could be. In taking the temperature while the boat was moving the thermometer made a little "bow wave" the light shone with a vivid green. This greenness is particularly beautiful—no hint of brown or blue in it, but a pure green and the algae are so minute that in small quantities of water the water hardly appears murky. This was a remarkable display of the sudden development of great quantities of small form of plankton and was doubtless brought about by the tremendous quantities of dissolved organic matter brought down into Thumb Lake by the thousands of decaying salmon in the river above. The "Balance of Nature" exemplified! What form now will follow the algae? At present the whole lake appears to be a pure culture of this form on a magnificent scale.[13]

After witnessing the huge run of sockeye salmon, the subsequent masses of salmon carcasses and their rapid decay, and an associated phytoplankton bloom in Thumb Lake, Rich quickly understood the possible importance of salmon-carcass nutrients to the fertility of Karluk Lake and nourishment of young sockeye. By late August and early September he recorded these ideas:

[Commenting about Karluk Lake, 20 August 1926] Also in view of the fact that "nitrogenous" samples need to be solvent in the water for the proper development of plant life, [could it] be that the presence of great numbers of dead [bodies] of the present fish affect the survival possibilities of the young fish . . . first the phyto- and second the zoo-plankton?

[Commenting about Karluk Lake, 27 August 1926] If successful growth and survival of the young salmon in the lake is dependent to greater or less extent on the presence of large numbers of dead [bodies] of the parent fish, it is quite conceivable that a good run in one year will affect the survival of the young fish produced from the spring run of the previous year, or even of the year before that (the 2nd year previous) as much or more, than it will the production of young from the eggs of the year of the big escapement.

[Commenting on the effects of pink salmon on Karluk Lake, 5 September 1926] If my idea—that an abundance of dead fish in the lake is desirable on account of fertilizing the water and thus producing an abundant plankton—if this is correct, it may be desirable to let humps into the lake even though they are not permitted to spawn in the main tributaries.[14]

The process of linking salmon-carcass nutrients to sockeye production in Karluk Lake originated from a number of fortuitous events unique to 1926. First, the huge sockeye run, possibly of similar size to those of the early fishery, produced many decomposing salmon carcasses along the tributaries and lake shore. Second, Rich, a well-trained biologist, by chance selected 1926 to observe the sockeye spawning grounds and began limnological studies at Karluk Lake. Fortunately, he visited the lake in July and August and saw the spawning salmon, carcasses, and phytoplankton bloom. Since his plans for 1926 included studies of the lake, he likely had prepared for this work by reading limnological papers and textbooks, this priming him to recognize the link between salmon-carcass nutrients and lake fertility. While awaiting passage south from Kodiak Island on 21 September 1926, he read the limnology textbook of Needham and Lloyd (1916) and pondered the relationship between lake plankton and juvenile sockeye growth. Unquestionably, he considered limnological studies worthy of further effort, and this work was pursued each field season while he led the Karluk research program during 1927–30. Since water chemistry measurements were lacking in 1926, Rich planned future studies to confirm or refute his salmon-carcass nutrient idea.

1927: Measurement of the Water Chemistry of Karluk Lake

After the preliminary work of 1926, Rich returned to Karluk Lake in 1927 with improved sampling gear and plans to study the lake's water chemistry. He spent over a month at the lake in 1927 (5 July–15 August), recording temperature profiles in all three basins, measuring transparencies, and collecting plankton and bottom sediments. Surface temperatures of Karluk Lake in 1927 were much cooler than in 1926, when a definite metalimnion (thermocline) had formed in mid summer. He used a standard 125 mm Secchi disk to measure transparencies, but thought these new data were incomparable with the 1926 readings made with a white plate of twice the diameter. His assistant, Seymour

[12] See footnote 6.

[13] See footnote 6.

[14] See footnote 6.

Smith, extended the 1927 sampling season well beyond the one month that Rich was present and regularly visited Karluk Lake between April and September, again measuring temperatures, transparencies, dissolved oxygen, total residues, and plankton.[15]

George Kemmerer, Professor of Chemistry at the University of Wisconsin, helped Rich with the limnological studies in 1927, measuring the water chemistry of Karluk Lake and its tributary lakes and streams. He erected a tent near the Camp Island cabin as a chemistry field laboratory. Kemmerer measured several chemical constituents, in particular focusing on nitrogen, phosphorus, and silicon since those nutrients were thought to stimulate phytoplankton growth.[16] Significantly, tributaries entering Karluk Lake had much higher nutrient concentrations downstream from salmon carcasses than did sites above salmon migration barriers. Sockeye carcasses increased nitrogen and phosphorus nutrients in these streams, even though the 1927 escapement was much smaller than in 1926. Thus, substantial quantities of nutrients entered Karluk Lake from the decomposing salmon carcasses; this influx fueled the food chain that produced the abundant plankton eaten by young sockeye salmon rearing in the lake.

Because of improved collecting gear in 1927, Rich was now confident of his plankton samples from Karluk, Thumb, and O'Malley lakes, and he obtained a wide size-range of zooplankton and phytoplankton by using both nets and a centrifuge (Juday et al., 1932). He again observed an August phytoplankton bloom in Thumb Lake—he claimed it was the green alga, *Chlamydomonas*—but found it less intense than in 1926 because fewer salmon carcasses contributed nutrients to the lake. Thumb Lake consistently had higher plankton densities than Karluk Lake, with O'Malley Lake being intermediate. For example, at Thumb Lake on 21 July Rich declared "this plankton haul was exceedingly rich—containing many times as much plankton as we have gotten from any other haul on Karluk Lake." Evidently, the planktonic densities of Thumb and O'Malley lakes were directly related to the number of salmon carcasses that added nutrients.

Rich also sampled the bottom sediments of Karluk Lake using an Ekman dredge in 1927. Kemmerer and Charles Black, Wisconsin Geological and Natural History Survey, later analyzed the chemical constituents of these sediments (Black, 1929; Juday et al., 1932). The fine bottom sediments were mainly accumulations of silica diatom valves that had settled out from the lake's phytoplankton. Albert Mann identified 67 species of diatoms in the sediments (Juday et al., 1932).[17]

Gilbert and Rich did not discuss salmon-carcass nutrients in their 1927 monograph on the Karluk River sockeye salmon, even though Rich was then actively investigating the idea. Perhaps their manuscript had already been submitted for publication when Rich first formulated his ideas on lake fertility in late 1926. Their 1927 paper only indirectly mentioned the lake's limnology, declaring that its large sockeye smolts were "partly due to their residence in Karluk Lake, partly, no doubt, to the unusually favorable conditions for growth which they find in this watershed." Even if it had been logistically possible to discuss salmon-carcass nutrients in the 1927 paper, the idea was then untested and needed further limnological evidence.

1928–1930: Continued Limnological Sampling of Karluk Lake

Rich spent less time personally collecting limnological data at Karluk Lake after 1927, though he continued to lead the USBF's sockeye salmon studies until 1930. Instead, he increasingly relied on his assistants, primarily students from Stanford University and other USBF employees, to collect the limnological and fisheries data at Karluk. Rich knew such data were needed to understand the sockeye salmon, but other fisheries studies in Alaska kept him from spending much time at Karluk. Also, his field assistants proved to be entirely capable of completing the field work. Rich did not visit Karluk Lake in 1928 and only briefly stopped in 1929 (5–15 July) and 1930 (8–18 July). His assistants collected the standard limnological data during 1928–30, but they made no further chemical measurements of the lake's nitrogen, phosphorus, and silicon.[18]

In 1932 Juday, Rich, Kemmerer, and Mann published the results of their 1926–31 limnological studies of Karluk Lake and formally proposed a linkage between sockeye salmon carcasses, nutrients, plankton

[15] Seymour P. Smith worked at Karluk Lake in 1927 much earlier (April) and later (September) than did Rich, and his field notes contain many limnological records. The Smith 1927 notebook was located at NARA, Anchorage, AK.

[16] Kemmerer George I. 1927 chemical data notebook (6 July–14 August). Located at NARA, Anchorage, AK.

[17] These Karluk Lake diatoms were eventually deposited in the U.S. National Museum, Washington, DC.

[18] In 1928 his USBF assistants Seymour P. Smith, Alan C. Taft, and Ed Maddox collected the lake data (temperatures, transparencies, plankton, and total residues), making two trips to the lake (9–16 July, 1–5 September).

Collecting plankton samples, Karluk Lake, July 1928. (Alan C. Taft, Auke Bay Laboratory, Auke Bay, AK)

production, and juvenile sockeye growth. Rich, a junior author of this landmark paper, apparently initiated the limnological study and did much of the early field work. Kemmerer measured the water chemistry, but spent only one month at Karluk Lake in 1927. Mann analyzed the diatoms in the bottom sediments collected by Rich, but never visited Karluk Lake. Chauncey Juday, a respected senior scientist and limnologist at the Wisconsin Geological and Natural History Survey, analyzed the plankton samples collected by Rich, but never visited Karluk Lake. It appears that Juday was placed as senior author of the 1932 paper because of his status and seniority, rather than for his field work or generating the original idea linking lake environment, salmon-carcass nutrients, and juvenile sockeye.

Besides their important results on water chemistry, Juday et al. (1932) were the first to describe the plankton communities of Karluk, Thumb, and O'Malley lakes from samples collected in July–September 1927–30. They used a closing plankton net (about 90 cm long) with a 12 cm diameter opening and #20 bolting silk[19] to collect 77 genera of zooplankton and phytoplankton: cladocera (5), copepoda (3), rotifera (17), protozoa (10), blue-green algae (10), green algae (17), and diatoms (15).

Rotifers were the most abundant zooplankton in Karluk Lake, followed by copepods and their early nauplii life stages, and then cladocera (Fig. 7-4). Rotifers often exceeded 100,000 per m^3, while mature copepods were usually less than 20,000 per m^3 and cladocera were less than 5,000 per m^3. Rotifers, though profuse, were small and unlikely to be selectively eaten by young sockeye salmon. Protozoa were also very abundant, but most were attached to copepods rather than being freely entrained in the water column. The most important taxa present as food for young sockeye were four macrozooplankters, the cladocera *Bosmina* and *Daphnia,* and the copepods *Cyclops* and *Diaptomus.* Of these, *Cyclops* was the most abundant. Cladocera and copepods were most numerous in the upper 50–70 m of Karluk Lake.

For the phytoplankton in the three basins of Karluk Lake, diatoms were usually the most abundant group, along with substantial numbers of green algae (Fig. 7-4). Diatoms often exceeded 3,000,000 per m^3, especially in the Thumb basin where a maximum of 67,000,000 per m^3 was found in July 1927, while green algae typically exceeded 2,000,000 per m^3. Diatoms and green algae were most abundant in the upper 20 m of the lake.

Thumb Lake had significantly higher densities of cladocera (10 times higher), rotifers (3 times higher), and diatoms (100 times higher) than did Karluk Lake. Incredibly, they recorded 7,386,500,000 diatoms per m^3 in Thumb Lake on 13 July 1930. The plankton community of O'Malley Lake was similar to that of Karluk Lake, except for having fewer copepods and much higher diatom densities (5 times higher). Besides the above results for net plankton, several centrifuge samples from Thumb basin and lake in 1927 revealed even higher abundances (up to 25 times) of diatoms and green algae. These forms, known as the nannoplank-

[19] Juday (1916) provided a full description of the closing plankton net used at Karluk Lake. Since the plankton net effectively strained only half the organisms in the water column, he multiplied the resulting densities by two. The #20 bolting silk has an aperture opening of 76 µm. All plankton densities were averages obtained from hauling the net from the lake bottom to surface in each of the three basins—south basin (0–125 m), Thumb basin (0–45 m), and north basin (0–50 m).

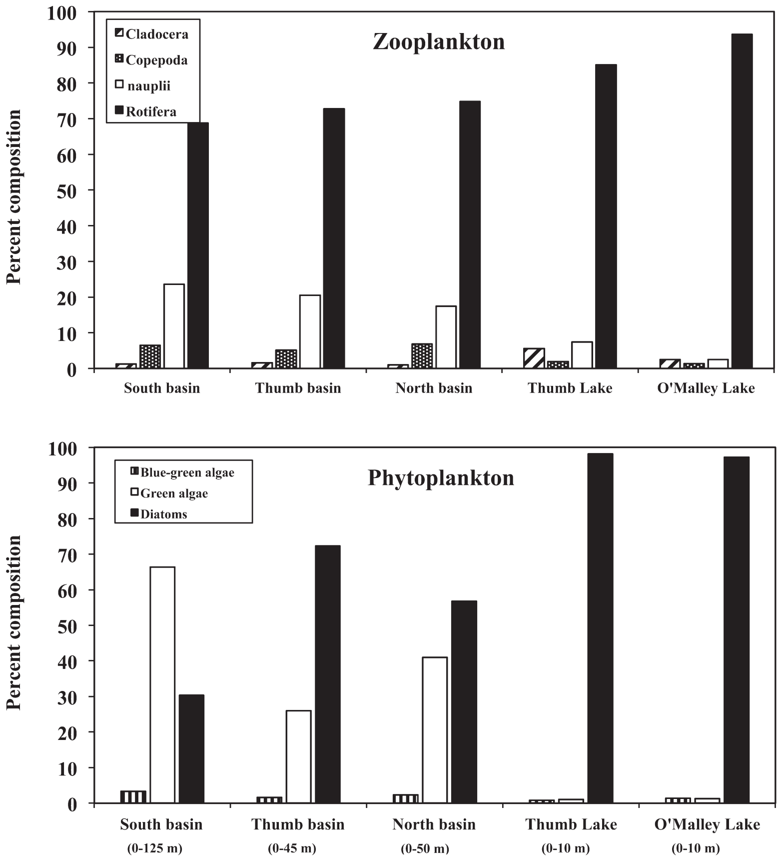


Figure 7-4. Percent composition of zooplankton and phytoplankton in the three basins of Karluk Lake, and Thumb and O'Malley lakes, July to September, 1927–30. Data from Juday et al. (1932).

ton, were so small that they passed through the fine 76 μm plankton net. The biologists concluded that the abundant plankton populations of the Karluk system were caused by the fertilizing effects of salmon-carcass nutrients.

Juday et al. (1932) presented the plankton density data with little analysis of the changes that occurred between early July and mid September. Yet, in retrospect, the pronounced seasonal fluctuations in plankton densities revealed important characteristics of the lake's trophic structure and dynamics (Fig. 7-5). Cladocera and copepods in Karluk and Thumb lakes were much more abundant (2–9 times) in September than in July, while diatoms and green algae were more abundant (3–10 times) in July than in September. This inverse seasonal relationship suggests that the crustacean macrozooplankton cropped the phytoplankton, which depended on the lake's nutrient fertility to maintain high levels of primary production. In contrast, rotifer densities in Karluk Lake were consistently higher in July than September, and at certain sites and years this group experienced ten-fold reductions in just 2–3 months. Seasonal changes in plankton abundance at O'Malley Lake were entirely opposite to those of Karluk and Thumb lakes, highlighting its different trophic structure and dynamics.

In conclusion, Rich's observations at Karluk Lake in 1926 sparked the idea that nutrients from decomposing salmon carcasses may enhance the lake's productivity, increase the forage base for young sockeye, and bolster future salmon runs. The limnological data collected in 1927, especially those on nutrient concentrations, reinforced his belief in the importance of salmon-carcass nutrients. Although fishery biologists have accepted and rejected the salmon-carcass nutrient idea over the past 75 years, it remains a viable theory of what sustains abundant sockeye runs at Karluk. Further, this idea stimulated limnological research at Karluk Lake for many years, including recent lake fertilization projects and studies of marine-derived nutrients in the lake's biota and sediments. Without a doubt, the limnological studies at Karluk Lake during 1926–31 established an early baseline of its physical, chemical, and biological characteristics; these data have provided a useful comparison with current lake conditions. Considerable evidence supports the idea that production of sockeye salmon at Karluk depends on the annual influx of nutrients transported into the lake in the bodies of returning adults.

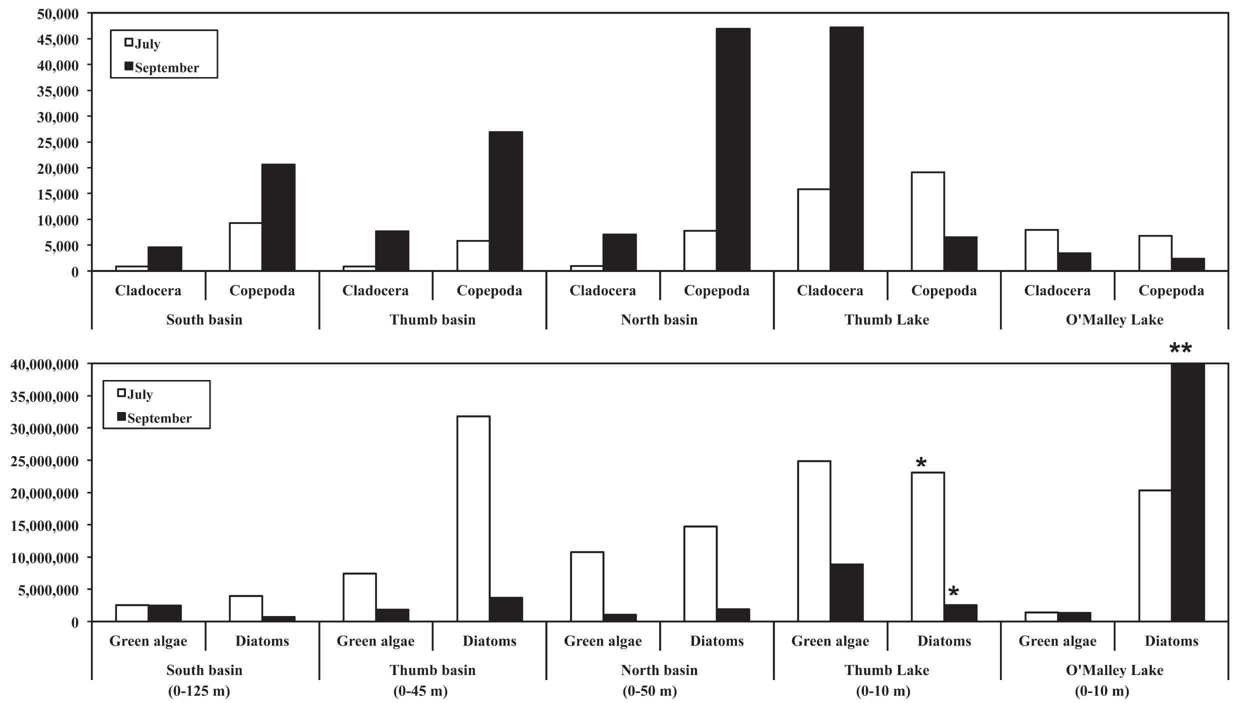


Figure 7-5. July and September densities (number per m³) of cladocera, copepoda. green algae, and diatoms in the three basins of Karluk Lake, and Thumb and O'Malley lakes, 1927–30. Data from Juday et al. (1932). *The true diatom densities in Thumb Lake are 10 times those shown. ** September diatom density in O'Malley Lake = 76,785,750 per m³.

1930–1937: Limnological Studies by Thomas Barnaby

Barnaby continued the limnological investigations of Karluk Lake during 1930–37. He was influenced by Rich, who showed him the collection methods when they worked together in 1930 and stressed the importance of the data for understanding the lake's productivity. Barnaby collected the standard set of limnological data from the three basins of Karluk Lake and its tributary streams and lakes for eight years; the data included spot water temperatures, temperature profiles, transparencies, and plankton. In addition, he often measured the total dissolved solids of lake water by evaporating known volumes and regularly monitored water levels and stream discharges. He visited the lake field station anywhere from two to six times each year to do this work (13–81 days total), but limnological studies were just one of many research topics he pursued at Karluk.

Tom Barnaby collecting limnological data, Karluk Lake, ca. 1934. (Joseph Thomas Barnaby, from Lynn L. Gabriel, Herndon, VA)

Tom Barnaby in the water chemistry laboratory, Camp Island cabin, Karluk Lake, ca. 1935. (Joseph Thomas Barnaby, from Lynn L. Gabriel, Herndon, VA)

Although Barnaby spent considerable time at the lake, he never mentioned seeing an algal bloom in Thumb Lake. And yet the water characteristics he recorded on 27 July–18 August 1934, when sockeye carcasses were very abundant, suggested that a bloom must have occurred. During those weeks the pH values exceeded 8.8 and transparencies dropped to 1.3 m. After heavy rains flushed the salmon carcasses downstream in late August, pH values rapidly declined to 7.2 in Thumb Lake.[20]

During 1935–37, Barnaby repeated the water chemistry study previously done by Kemmerer at Karluk Lake in 1927. He set up a field chemistry laboratory in one room of the Camp Island cabin and stocked it with glassware, chemicals, reagents, and an apparatus for making distilled water. He spent considerable time analyzing the nitrogen, phosphorus, and silica nutrients of lake and stream waters, in addition to the pH, free carbon dioxide, and dissolved oxygen. As in 1927, streams with salmon carcasses had higher levels of phosphorus than did Karluk Lake or the same streams above salmon migration barriers. Also, tributary streams had higher silica levels than did Karluk Lake. From these results, Barnaby (1944) concluded that phosphorus and silica may limit phytoplankton production in Karluk Lake. He understood that some of these nutrients, largely coming from salmon carcasses, influenced the lake's productivity:

> [Speaking of Karluk Lake] A factor to be considered in relation to the optimum magnitude of the escapements of red salmon is the addition to the lake water of phosphorus and other inorganic salts from the bodies of the fish which migrate into the watershed to spawn. Prior to the inception of the commercial fishery, Karluk Lake received a large supply of chemical compounds each year because practically all of each season's run of fish proceeded to the lake and its tributaries to spawn and die. As soon as the commercial fishery began, the spawning escapements became less, and not only were there fewer spawners available to deposit eggs in the gravel, but the yearly increment of chemical compounds to the water was considerably decreased.
>
> The yearly increment of soluble phosphorus is dependent, very largely, upon the number of spawning fish which enter the lake each year. There was from 1 ½ to 10 times the concentration of phosphorus in the water at the mouths of the streams as in the water of the same streams, on the same dates, above the area where spawning and spawned-out salmon were found. Furthermore, a part of the salmon spawn along the beaches of the lake and eventually die, and the carcasses, together with the carcasses which drift downstream into the lake from the tributaries, decompose and the phosphorus contained therein becomes available to the phytoplankton. A shortage of phosphorus in the lake water would inhibit the growth of all forms of phytoplankton.
>
> It is apparent that a study of the chemical analyses of the lake water and of the stream waters that both phosphorus and silica are being absorbed, during the summer months, by the phytoplankton as fast as they become available, for otherwise the concentrations of these chemicals in the lake water would approach that found in the streams. Since concentrations of these chemicals in the lake water during most of the summer was less than a measurable amount, it is evident that they must be limiting factors in the production of the phytoplankton and may possibly be affecting indirectly the growth and survival of the red salmon fingerlings of Karluk Lake.

[20] Thomas Barnaby recorded limnological data at Karluk Lake in 1930–37 in five field notebooks. Located at NARA, Anchorage, AK.

Barnaby (1944) formally published his water chemistry results from 1935–36, but for unknown reasons excluded the 1937 measurements.[21]

1938–1942: DeLacy and Morton Period

Barnaby did not collect limnological data prior to leaving the Karluk research project in July 1938, but DeLacy, the new USBF research leader at Karluk, continued this work during 1938–42. In August–September 1938, USBF seasonal biologist Wendell Pike measured temperature profiles, pH, and water levels at Karluk Lake. He observed an algal bloom on 22 August and stated that "Upper Thumb—lake and river is very dirty and water has putrid taste".[22] DeLacy and his assistant Morton collected extensive limnological data from all three basins of Karluk Lake and from its tributary streams and lakes during 1939–42. Their measurements included spot temperatures, temperature profiles, transparencies, pH, phosphorus, silica, nitrate, carbon dioxide, dissolved oxygen, and plankton. They diligently sampled at each collecting site on 7–12 dates in 1940 and on 23 dates in 1941.[23] In addition, they measured the water chemistry of several tributaries (Alder, Cottonwood, Halfway, Upper Thumb, Meadow, Cascade, and O'Malley) and operated a recording thermograph at the Lower Thumb River during 1939–41 and at Karluk Lake in 1942. Surprisingly, the large mass of limnological data from 1938–42 was never analyzed or presented in formal publications and agency reports.[24]

Notwithstanding the conscientious efforts of DeLacy and Morton, the USBF official correspondence and research plans for 1938–42 seldom stated the rationale for collecting the limnological data, though Rich's idea of a link between carcass nutrients and salmon productivity still must have been influential. Yet few biologists or officials then discussed the importance of lake nutrients or the possibility of fertilizing Karluk Lake to enhance its sockeye runs. One brief exception occurred in 1941, when Morton mentioned that he and DeLacy "discussed fertilization of Lake by plane or truck with fish heads & guts".[25] As a result, most of the detailed limnological work at Karluk from this period was filed away as raw data and never used.

1943–1946: Absence of Limnological Collections

The importance of collecting limnological data at Karluk Lake waned after 1942 and none were gathered during 1943–46. During these years, the research biologists devoted much of their field effort to maintaining the counting weir at the Portage, transporting lumber and supplies to the new weir site near the lake's outlet, and building a new weir cabin and research facilities. They also conducted sockeye research at the lake, but limnological measurements were absent. Nevertheless, Rich's continued enthusiasm for studies of Karluk Lake was about to re-ignite this work.

1946–1949: Preliminary to the Lake Fertilization Experiment

Rich's idea that salmon-carcass nutrients affected the fertility and young sockeye of Karluk Lake was revived during 1946–49 when Shuman led the FWS sockeye studies. In late 1945 Shuman analyzed the escapement-return relationship for Karluk's sockeye salmon; before the results were published, he sent the manuscript to Rich for review.[26] Rich declared that Shuman's analysis, which had used data from 1921–39, was inadequate because by this period the sockeye salmon runs had already been depleted. Instead, he argued that the long-term decline in Karluk's sockeye run had been caused by a persistent reduction in lake fertility, as fewer salmon carcasses contributed fewer nutrients to the lake. That is, nutrient depletion had reduced the lake's

[21] USBF 1937 data notebook of Karluk Lake water temperatures and chemistry. Located at NARA, Anchorage, AK.
[22] Pike, Wendell. 1938 notebook. Located at NARA, Anchorage, AK.
[23] 1) The 1940 collection dates are from William M. Morton 1939–41 notebooks. Located in personal papers of Robert S. Morton, Portland, OR.
2) The 1941 data records are from FWS 1941 data notebook. Located at NARA, Anchorage, AK. The 1941 Karluk Lake data were collected from 25 June to 12 September at Station 1 (0 to 100 m) and Station 2 (0 to 40m).
[24] Apparently, all limnological data from 1938–42 remain as raw numbers. Field notebooks and monthly reports document that limnological collections were made (See footnotes 22 and 23; USBF 1938–43 monthly reports located at NARA, Anchorage, AK). Morton often noted that limnological work was done, but seldom recorded the raw data in his three notebooks (1939–41). The data for 1941–42 is located at NARA, Anchorage, AK. Limnological data may also exist in DeLacy's field notebooks, but their location is unknown.
[25] Morton, William M. 1939–41 notebooks (12 June 1941). Original notebooks in personal papers of Robert S. Morton, Portland, OR.
[26] Shuman, Richard F. 1945. Observations on escapements and returns of red salmon at the Karluk River. FWS, Division of Fishery Biology. Unpubl. report. 17 p. Located at ABL, Auke Bay, AK.

plankton productivity and the growth and survival of juvenile sockeye:

> [Discussing Karluk River sockeye salmon] The result of this brief and wholly preliminary examination of the catch statistics in recent years led me to examine similarly the whole record. . . . The general picture is clearly one of constant depletion. There is no evidence from the catch data that the regulation of the fishery under the White Act of 1924 has had the slightest effect in preventing further depletion, to say nothing of providing conditions under which the run might build back toward its former size. This, I believe, is of fundamental importance—not only to the management program at Karluk, but to the general principles of salmon conservation. What is the explanation? Here is what may well be the most important problem facing those who are today involved in studying salmon problems.
>
> It seems to me that the most probable explanation is that there has been a progressive reduction in the capacity of the Karluk system to produce red salmon—a reduction that is due to a change (probably gradual) in those ecological conditions that were, in the early years, so exceedingly favorable. Such a reduction might well have come about by a constantly reduced fertilization of Karluk Lake by the dead bodies of the parent fish—the reduced fertilization being due in turn to the great numbers of adult fish that were taken out of the runs by the commercial fishery. The effect of such reduced fertilization might well be gradual extending over a long period of years, as stored chemicals are depleted. This would result in a gradual reduction of the number of young that the lake would produce and this would limit the size of the runs of adults. In terms of the population curve it would result in a gradual reduction of the maximum population. . . .
>
> Now, if it is true that there has been a gradual reduction in the potential production at Karluk—a process that is still continuing—we can understand why the management of the fishery under the White Law has failed to halt depletion, why the data of the last few years show that the maximum population is only about 1–¼ million, and why there has been a negative correlation between escapement and surplus during the past twenty years or so. All of these facts fit logically into the picture.[27]

Based on his nutrient reduction theory, Rich believed that Shuman's escapement goal of 350,000 to 500,000 fish was too low and argued for a much higher goal of 2,000,000 fish to restore the lake's fertility:

> But it seems to me that it would be folly to go still farther in the same direction by still further reducing the escapement. I believe that we should increase rather than decrease the escapement but I do agree that a fixed escapement rather than one determined on a percentage basis would be highly desirable—in fact the only way in which provision can be made for the real recovery of this run. I suggest, tentatively, that the escapement be fixed at approximately half the original population, on the theory that the greatest increment will be provided at that level—an increment that may be less than 50 per cent of the total run. The original population was certainly well in excess of three million fish because the average catch alone for the seven years 1888 to 1894 was in excess of this figure and there was still enough escapement to provide an average catch in excess of two million for the next seven or eight years. If we assume conservatively that the average run originally was four million, we could not be far wrong. I suggest therefore that we endeavor to provide an escapement of two million. I realize that this cannot be done immediately. If the figures are correct there are not that many fish in the present runs, but I should like to see an effort made to build in that direction.[28]

After Rich critiqued Shuman's manuscript in April 1946, considerable discussion ensued within the FWS about the nutrient-depletion idea, the direction of the Karluk research program, and the possibility of rehabilitating the sockeye run.[29] Shuman and Rich, along with Barnaby and Kelez, met in Seattle in May 1946 to discuss these ideas further. Rich must have convinced the others about his nutrient-depletion theory since limnological data were subsequently collected with renewed vigor. Further, the purpose for collecting these data was now focused on the eventual goal of fertilizing Karluk Lake to enhance its sockeye salmon productivity:

> [Rich discussing the nutrient-depletion idea for Karluk Lake] While in Seattle I had a long discussion of the problem with Shuman, Kelez and Barnaby. I believe that the general features of my analysis were accepted without many reservations; but my proposal to increase the escapement as a means of increasing the fertility of the lake met with the identical response that you gave in your letter, namely, that we should, instead keep the escapement low and attempt to refertilize the lake artificially by introducing fertilizer. To this suggestion I agreed, with the understanding that the program be approached as an experiment.[30]

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[27] Memo (22 April 1946) by Willis H. Rich, Consultant, Salmon Fishery Investigations, on Shuman's manuscript "Observations on escapements and returns of red salmon at the Karluk River." Located at NARA, Anchorage, AK.

[28] See footnote 27.

[29] Discussions included Richard Shuman and several FWS officials, including Elmer Higgins (Chief, FWS Division of Fishery Biology), Lionel Walford (FWS Director of Research), George Kelez (Chief, FWS Alaska Fishery Investigations), Ralph Silliman (Chief, FWS Section of Anadromous Fisheries), and Clarence Rhode (FWS Regional Director).

[30] Letter (11 May 1946) from Willis H. Rich, Consultant, Salmon Fishery Investigations, to Elmer Higgins, Chief, Division of Fishery Biology, FWS, Washington, DC. Located at NARA, Anchorage, AK.

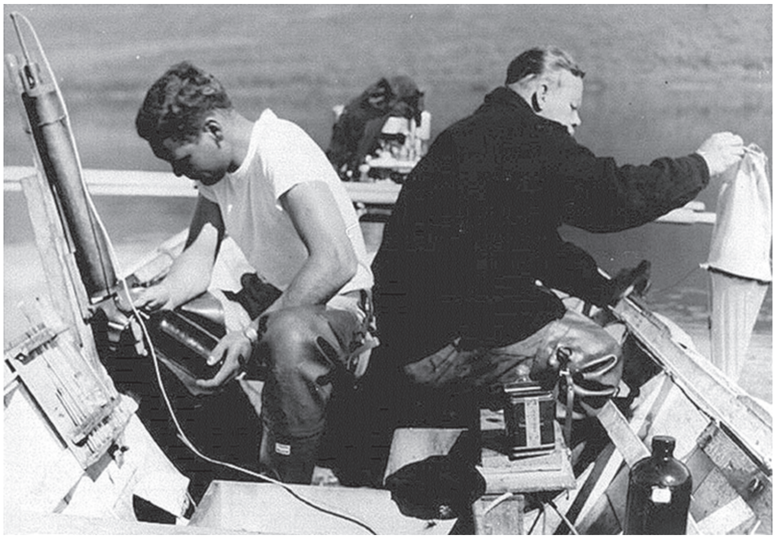
Kelez summarized the 1946 discussions about nutrient depletion in Karluk Lake and the future actions needed by the FWS to restore its sockeye salmon:

> In general, we agreed that all red salmon runs which have been highly exploited have suffered a progressive decline in abundance and that theoretically this decline must be due to progressive lessening of the fertility of the lakes, which in turn is associated with reduction in numbers of adult carcasses available for replenishing vital materials in the lakes. Because of the lingering of chemicals in the lakes, and particularly bottom deposits which are only partially redistributed by the vernal mixing, a progressive decrease in fertility may exist over a considerable period before its effects become marked. Under these conditions the high proportionate return from small escapements becomes easily understandable, as does the limited return from a large escapement following a number of years of small seedings.
>
> Mr. Shuman's conclusions as to the benefits of limiting the spawning population are perfectly valid so long as fertility is maintained by other means. Early in the discussion I had introduced the not-entirely facetious remark that we might find it necessary to obtain large escapements into the lake and weir the spawning streams so that only a small proportion of the adult fish were allowed to spawn, thus utilizing the unspawned adults purely as fertilizer. This, I believe, was essentially the case in primitive times when the escapements were so large that overspawning on the gravels reduced the number of fry surviving to a small part of the actual egg deposition.
>
> The adoption of Mr. Shuman's proposal without other means of fertilization would reduce the level of the population in a few years to a new low level governed by the correspondingly reduced fertility of the lake, and our situation would be similar to that of the present time after a few years of relatively high production (proportionately) from the reduced escapements. Dr. Rich's request for a large escapement is perfectly valid for increasing fertility so long as the number of progeny entering the lake do not increase, otherwise they drain the lake of nutrients as fast as they are deposited and their proportionate production of surpluses will be as low as large escapements of recent years have produced.
>
> We therefore considered a reduced escapement accompanied by artificial fertilization. To improve fertility in the amount represented by the difference between Dr. Rich's 2,000,000 fish and Mr. Shuman's 400,000 would, of course, require a very considerable amount of material. Super-phosphate was suggested by Mr. Barnaby. . . . but it is questionable that this is the sole factor necessary. Organic fertilizers may be necessary to supply other vital elements and it is conceivable that we might use the seal-meal from the Pribilofs for this.
>
> Mr. Barnaby and Mr. Shuman both felt that the salmon packers of the district would be willing to contribute to such a program. It was suggested that they might be asked to contribute one pound of fertilizer for each fish taken above the number which would have been caught with the larger escapement in effect. Until some such agreement is effected it appears unwise to lower the escapement since we cannot carry the financial burden ourselves. A road to Karluk Lake would also be essential to such a program.
>
> We should proceed to test this theory as soon as possible. Karluk, because of the long series of observations and the counting facilities would be ideal; if the cost of the experiment is too great, then we might use one of the very small Bristol Bay lakes where fertilization would be feasible.
>
> The implications of this theory are far-reaching. It may well explain why we have not bettered the Alaska runs, and particularly at Karluk, in over twenty years of management. If this is the basic factor controlling red salmon production, then we must theoretically either adopt fertilization everywhere or build up the populations to the point where overspawning occurs. If this is not done, then we may expect a continuation of the downward trends that have become especially apparent in recent years, both at Karluk and in Bristol Bay.[31]

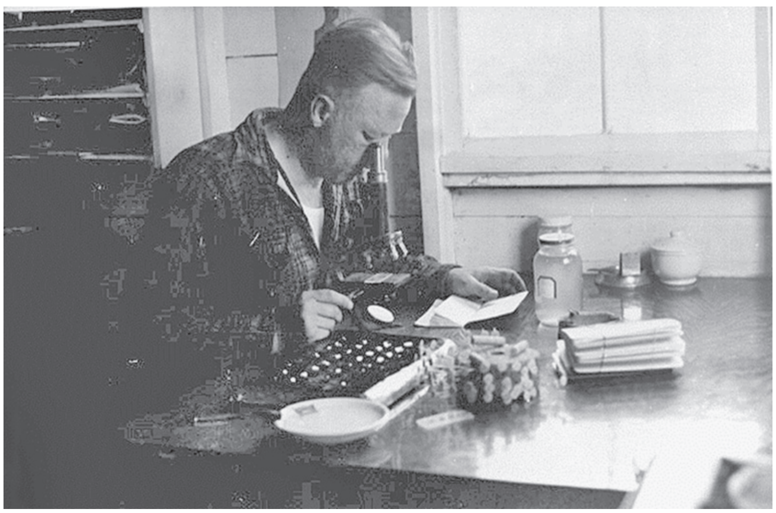
Obviously, Shuman's ideas about sockeye salmon production at Karluk were greatly affected by his interaction with Rich and the events during 1946. In fact, he readily accepted many of Rich's ideas and increased the escapement goals for spring- and fall-run sockeye to 350,000 each. In late 1946, Shuman sought additional funds from the FWS to expand the limnological studies at Karluk Lake, purchase better boats, and build a new field laboratory. With the long-term goal of fertilizing the lake, he began gathering baseline data on its physical, chemical, and biological properties.

Collection of limnological data began in earnest in 1947 and continued for several years from all three basins of Karluk Lake and the two tributary lakes. Biologists measured water temperature profiles, transparencies, water chemistry, and plankton and operated a continuous recording thermograph in the upper Karluk River. Shuman collected and identified plankton samples from all three lakes; his assistant, Philip Nelson, converted the Camp Island cabin into a water chemistry laboratory and regularly measured several lake nutrients (nitrogen, phosphorus, and silica) at different lake depths. Because of their interest in the limnological program and future lake fertilization, Rich, Barnaby, and Kelez visited Shuman and Nelson at Karluk Lake in 1947–48 to monitor the lake studies and offer advice and technical assistance. Although more than 20 years had passed since Rich had actively worked

[31] Letter (6 May 1946) from George B. Kelez, In Charge, Alaska Fishery Investigations, Seattle, WA, to [Elmer] Higgins, via Director, FWS, Washington, DC. Located at NARA, Anchorage, AK.



Richard Shuman (right) collecting water samples and plankton, Karluk Lake, July 1948. (Richard F. Shuman, Auke Bay Laboratory, Auke Bay, AK, FWS–1281)



Richard Shuman identifying lake plankton samples and determining the age of sockeye salmon scales, Karluk Lake cabin, August 1948. (Richard F. Shuman, Auke Bay Laboratory, Auke Bay, AK)

at Karluk, his enthusiasm for this productive ecosystem was unabated and in 1949 he built Shuman a large plankton net to aid the project. Without a doubt, limnological sampling was an important part of the research program at Karluk Lake in the late 1940s. Even so, in spite of the renewed efforts to amass a comprehensive set of limnological data during 1947–49, little of this information was ever published or used.[32]

During these years, the limnological work at Karluk Lake was typically done in May–September; the biologists left the lake by early October as the weather deteriorated and winter approached. But in 1948 FWS seasonal biologists Arthur Freeman and Francis Walter sampled the lake through October–November.[33] Little was then known about the lake's limnology in late autumn or early winter, making their observations unique. They collected the full range of limnological data from each of Karluk's three basins and from Thumb and O'Malley lakes, including water temperature profiles, transparencies, water chemistry (phosphorus, nitrogen, silica, hardness, bound and free CO_2, dissolved oxygen), and plankton. They also operated the thermograph in the upper Karluk River. All three lakes rapidly cooled in October–November until little or no thermal stratification existed. Thumb and O'Malley lakes became ice-covered by mid November, well before ice formed on Karluk Lake (Table 7-3). When Freeman and Walter left the field station on 30 November, surface water temperatures of Karluk Lake were 4–5°C and the upper Karluk River was ice-free. As they proceeded downriver, however, water temperatures declined until the river became ice-covered near Barnaby Ridge, about 4 km upstream of the Portage.

[32] The limnological data from 1947–49 exist as raw numbers at NARA, Anchorage, AK.

[33] Freeman, Arthur. 1948 notebook. Original notebook in personal papers of Arthur Freeman, Indianapolis, IN.

Table 7-3
Water temperatures (°C) and ice formation in the Karluk Lake area, October–November 1948.[1] (d = water temperature at depth (120 m); s = surface water temperature; u = uniform water temperature from surface to bottom)

1948 Date	Karluk Lake South basin	Karluk Lake Thumb basin	Karluk Lake North basin	Thumb Lake	O'Malley Lake	Upper Karluk River
10-Oct		7.2u				
11-Oct				4.2u		
13-Oct					4.9	
22-Oct						6.0
25-Oct	6.6s–6.0d					
26-Oct				3.7u		
27-Oct		6.2u	6.4u			
28-Oct					4.1	
4-Nov					1/4 ice cover	
9-Nov					2.5	
10-Nov	5.9s	4.9d				
11-Nov				2.6s–2.4d		
12-Nov			5.6u			
15-Nov				2/3 ice cover		
18-Nov				1/4 ice cover		
19-Nov				solid ice cover		
20-Nov				8 cm ice		
21-Nov					10 cm ice	
23-Nov		3.9s	4.6s			
26-Nov	4.6u					
27-Nov				25 cm ice		
30-Nov						ice cover at Barnaby Ridge

[1] From Freeman 1948 notebook. Original notebook in personal papers of Arthur Freeman, Indianapolis, IN.

They discovered that the slightly warmer waters that discharged from the lake's outlet kept the upper river ice-free in late autumn. This warmer ice-free zone affects late spawning sockeye and coho salmon and the incubation rates of buried salmon eggs.

Another finding of Freeman and Walter's work was the increased water transparencies in all three basins of Karluk Lake (11.5–13.2 m) and Thumb Lake (5 m) in October–November.[34] By comparison, water transparencies in May–September had been much less in Karluk (5–10 m) and Thumb (1–3 m) lakes. Phosphorus and silica concentrations increased in October–November, and these often were the highest values recorded in 1948. Freeman and Walter believed that plankton populations were less dense, causing the increased transparencies and nutrients.

While Shuman did not mention limnology or lake fertilization in his initial 1945 Karluk manuscript, he soon incorporated Rich's ideas about salmon-carcass nutrients and the lake's declining fertility into revised manuscripts.[35] He recommended further limnological studies of Karluk Lake, including artificial fertilization experiments. His final manuscript discussed many factors that might affect the freshwater survival of young sockeye and concluded that the long-term decline in salmon-carcass nutrients had reduced the planktonic food supply:

> [Concerning factors affecting the juvenile sockeye of Karluk Lake] Of all the variables that have now been considered, this fertility is the only one that is known to have changed in such a way as to have been responsible for the continuous downward trend in abundance of the Karluk red salmon. Throughout the years of fishing there has been a continuous decline in this natural fertilization of the lake, and the evidence available makes it appear likely that there has been a corresponding decrease in the amount of available food.

[34] This high transparency of Thumb Lake was measured on 27 November 1948 through 25 cm of ice.

[35] 1) Shuman Richard F. 1950. Biological studies of the red salmon *Oncorhynchus nerka* (Walbaum) of the Karluk River, Alaska. A report on the trends in abundance, with a discussion of the ecological factors involved. Unpubl. report. 73 p.
2) Shuman, Richard F. 1951. Trends in abundance of Karluk River red salmon with a discussion of ecological factors. Manuscript prepared for Fish. Bull. 71(52). Unpubl. report. 56 p. Both reports located at ABL Office Files, Auke Bay, AK

Thus, while it is natural to suspect that the decline in abundance at Karluk has been caused by something related to the continued decrease in the size of spawning escapements, it does not follow that a decrease in the number of eggs placed in the gravels has been the fundamental cause. Rather, the lowered productivity, while caused by a decrease in escapements, seems to be an indirect result, and probably has been brought about by the decreased amounts of organic fertilizer given to the lake each year by decomposing carcasses of spawned-out fish.[36]

Shuman estimated that prior to commercial fishing at Karluk in 1882, about 4,000,000 sockeye salmon annually returned to the lake. While many of these may not have been effective spawners because of limited spawning space, the salmon carcasses added about 20,000 kg of soluble phosphorus to the lake, a major nutrient inflow that sustained the lake's plankton. Thus, Shuman recommended that Karluk Lake be artificially fertilized to restore its productivity, but that this should first be tested on a smaller lake to learn the best methods, fertilizers, and concentrations and how such an enrichment might affect the lake's limnology and sockeye salmon:

[Concerning the possible fertilization of Karluk Lake, 1951] The information now available indicates that artificial fertilization of the lake waters would be a basically sound program, and that plankton growth can be stimulated in this manner. It has not been proved that the lack of food is the cause of the downward trends in abundance at Karluk, but the evidence considered seems to indicate that it is. The present low level of abundance of red salmon is alarming, and the downward trend which has been in evidence for six decades can be expected to continue until some counteraction is taken. In view of the urgent need for rehabilitation it appears reasonable to accept the risks involved, and to institute immediately the initial steps of a comprehensive fertilization program as described here.[37]

By early 1949 the FWS had decided to experimentally fertilize a small lake on Kodiak Island as a first step toward eventually fertilizing Karluk Lake. Shuman met with Henry Eaton and Pat Cannon, United Fishermen of Alaska of Kodiak, in May 1949 to discuss the fertilization project and received $1,000 in funding from the fishermen's union, support that was given annually for at least the next five years. In July several FWS officials visited Shuman and Nelson at Karluk Lake to discuss the future enrichment work and urged them "to bear down on fertilization and mathematical examination of data."[38]

[36] See footnote 35 (2).
[37] See footnote 35 (2).
[38] Shuman, Richard F. 1949 notebook (17 July). Located at NARA, Anchorage, AK.

Hence, in mid July Shuman and Nelson began testing water samples by adding different chemicals to light and dark bottles and then incubating them in Karluk Lake. They made an aerial reconnaissance of Kodiak and Afognak Islands on 28 July 1949 to find a suitable small lake for the fertilization experiment. Their first possibility, a lake near Izhut Bay on Afognak Island, was rejected since its outlet stream was then dry. Most lakes they surveyed were either too large, had no outlet, or were too far from the coast to provide good access. Finally on 30 July, they located Bare Lake, about 25 km SW of Karluk Lake; it appeared to be suitable for the fertilization experiment. On their first visit to Bare Lake, they measured its physical dimensions, maximum depth, transparency, water chemistry, and water temperature profile, and collected a plankton sample. The lake had a small natural population of sockeye salmon that spawned in the littoral zone; the few inflowing creeks and springs were too small for adult sockeye to enter.

After choosing Bare Lake for the experiment, Shuman and Nelson spent the rest of the 1949 field season getting ready for the first artificial fertilization in 1950. Though they wanted to collect pre-fertilization baseline data on Bare Lake, FWS officials urged them to start the experiment as soon as possible. Therefore, in August 1949 Shuman and Nelson ran preliminary tests of different fertilizers added to bottles of Bare Lake water and incubated them in Karluk Lake. Though Shuman actively participated in the 1949 planning for the experiment, this was his last field season at Karluk Lake, and Nelson was placed in charge of all Karluk and Bare lake studies. To prepare for the fertilization experiment, Nelson returned to Seattle in late August and conferred with W. T. Edmondson, a professor and limnologist at the University of Washington.

1950–1956: Bare Lake Fertilization Experiment

Bare Lake, a tributary of the Ayakulik River on SW Kodiak Island, is relatively small when compared with Karluk Lake:

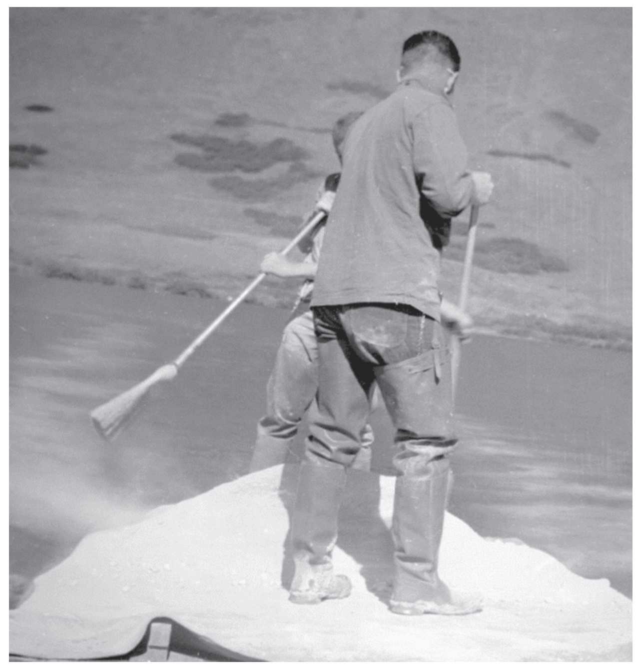
	Area (km^2)	Volume ($m^3 \times 10^6$)	Mean depth (m)	Maximum depth (m)
Bare Lake	0.5	2	4.0	7.5
Karluk Lake	39.5	1920	48.6	126.0

Being shallow and exposed to the winds, Bare Lake typically had uniform water temperatures from surface to

Bare Lake, used by the Fish and Wildlife Service in their artificial fertilization experiment, SW Kodiak Island, May 1954. (Clark S. Thompson, Shelton, WA)

bottom. Before the fertilization experiment began, only a few hundred or thousand adult sockeye salmon returned to spawn in the lake each year. Besides sockeye, the lake was inhabited by adults or juveniles of threespine stickleback, Dolly Varden, coho and Chinook salmon, coastrange sculpin, and steelhead.

During 1950–56, nitrogen and phosphorus fertilizers were added to the littoral zone of Bare Lake each June–July, and the water chemistry, plankton, and fish populations were monitored (Nelson and Edmondson, 1955; Nelson, 1958, 1959). Biologists loaded the solid fertilizers onto a small floating platform, mixed the different granules together, and then swept them into the lake as the boat slowly moved along the shoreline. The added fertilizers—sodium nitrate and either super phosphate (19%) or ammonium monohydrogen orthophosphate—had been estimated to increase the concentrations of nitrate to 0.25 mg/l and of phosphate to 0.05 mg/l. Nelson expected the fertilizers to quickly stimulate phytoplankton production, which should increase the zooplankton and bottom fauna foods of young sockeye. He then expected that enhanced food supplies would enhance the growth and survival of juvenile sockeye and eventually to augment the numbers of adults that returned to the lake. The artificial fertilizers added to the lake would supplement the nutrients released from any decomposing salmon carcasses.



Sweeping chemical fertilizer into Bare Lake as a boat towed the fertilizer raft along the shoreline, ca. 1952. (Philip R. Nelson, Largo, FL)

After Bare Lake was fertilized each year, many distinct changes occurred in the water chemistry and biota; most variations matched Nelson's predictions. Primary production increased by 2.5 to 7 times and phytoplankton populations greatly increased, turning the lake green. Water transparencies decreased from about 6 m before fertilization to less than 2 m after enrichment. As phytoplankton depleted the lake's carbon dioxide, pH values rose from 7.0 to 9.0. Nitrate and phosphate concentrations rapidly declined as phytoplankton utilized the added fertilizer nutrients. Zooplankton populations failed to increase during 1950–52, though some taxa increased their egg production. Because of their longer life cycles, the response of zooplankton to lake fertilization was expected to be slower than for phytoplankton. In fact, one year after the last fertilization in 1956, zooplankton populations were three times larger than in 1952 (Raleigh, 1963).

Mixing chemical fertilizers before adding them to Bare Lake, ca. 1952. (Philip R. Nelson, Largo, FL)

Philip Nelson collecting water and plankton samples at Bare Lake, February 1955. (Auke Bay Laboratory, Auke Bay, AK)

Nelson monitored the bottom invertebrate fauna of Bare Lake during at least some fertilization years, but these results went unpublished and it remains unknown if enrichment affected benthic populations. This lapse was unfortunate since the young sockeye of Bare Lake fed mainly on benthic macroinvertebrates during the summer, especially on the abundant chironomid larvae (Nelson, 1959). This benthic feeding behavior in Bare Lake highlighted a possible significant difference in its trophic structure from that of Karluk Lake, where juvenile sockeye fed on zooplankton. The summer diets of Bare Lake's young sockeye also included chironomid pupae and adults, and surprisingly, a few fish ate stickleback eggs. Winter diets, based on 13 juvenile sockeye collected from the ice-covered lake on February 1955, were ostracods and copepods, plus smaller amounts of cladocerans, insect larvae, and algae (Nelson, 1959).[39] During his winter visit to Bare Lake, Nelson caught many juvenile sockeye by fishing through the ice using salmon-egg bait, which showed that these young fish fed opportunistically.[40] He also caught a juvenile coho (343 mm) that had eaten three young sockeye (70 mm).

Despite the uncertain study results for the zooplankton and benthos, Nelson (1959) found that fertilizing Bare Lake increased the growth of juvenile sockeye salmon, including both first-year young and smolts. In fact, the smolts had increased by more than 30% in length and 150% in weight by 1955. Further, a direct relationship existed between phytoplankton primary production and juvenile sockeye size. Fertilization also increased the freshwater and ocean survival of the sockeye salmon. Even so, when fertilization ended in 1956, the number of adult sockeye salmon that returned to Bare Lake had not increased (Table 7-4). The enrichment experiment, therefore, affected at least part of the lake's food chain and had apparent benefits to juvenile sockeye, but, disappointingly, adult sockeye numbers seemed to be unaffected.

When evaluating the overall effectiveness of any lake fertilization project, an important consideration beyond the impacts on sockeye salmon is how the enrichment affects other resident fish species. Nelson (1959) only briefly discussed this topic for the three most abundant fish populations (besides sockeye) in Bare Lake: threespine sticklebacks, coho salmon juveniles, and Dolly Varden. He was not successful in measuring stickleback populations using mark-and-recapture samples, but did determine that stickleback growth seemed to be unaffected by the fertilization. The number of coho salmon smolts may have increased during the fertilization years, but such evidence was inconclusive (Table 7-4). Raleigh (1963) claimed that both coho salmon and Dolly Varden populations increased between 1952 and 1957, but without pre-

[39] Letter (15 March 1955) from Phil [Nelson], Seattle, WA, to M. P. Shepard, Pacific Biological Station, Nanaimo, BC. Located at NARA, Anchorage, AK.

[40] Nelson, Philip R. 1955 notebook (21–24 February). Located at NARA, Anchorage, AK.

Table 7-4
Bare Lake fish populations, 1950–61.

Year	Sockeye Adults	Sockeye Smolts	Dolly Varden Migrating	Dolly Varden In lake	Coho smolts	Comment
Fertilization years						
1950	551	10,199			1134	
1951	52	4503	2733		2389	
1952	382	8620	3905		1781	
1953	250	5058	797		2014	
1954	232	12,189	1058		3341	
1955	420	24,100	2300	4200	3247	
1956	347	6525	2777	6100	2946	
Post-fertilization years						
1957	225	7611		8200	2664	Very low water in Bare Creek
1958	1300	251–594				Minimal study in 1958
1959	137	1781		4850	ca. 1800	Very low water in Bare Creek
1960	419	2900		3400	>2800	
1961	531	1813			2513	Measured to 30 June

fertilization studies of these fish populations it was difficult to tell if significant changes occurred.

Nelson's fertilization experiment at Bare Lake was truly pioneering, as this idea had never before been attempted in Alaska. At the time, the consequences of adding artificial fertilizers to an Alaskan salmon lake were unknown. Would nutrient additions improve the growth and survival of young sockeye salmon, and what changes might occur in the lake's limnology?

Nelson demonstrated at Bare Lake significant linkages between nitrogen and phosphorus nutrients, phytoplankton abundance and productivity, and growth and survival of juvenile sockeye. Benefits to adult sockeye salmon were lacking, but perhaps the results he obtained were the most that could have been expected from the experiment. Because Bare Lake was relatively small and had a small natural run of sockeye salmon, the number of adults that returned each year was highly vulnerable to chance events, such as the vagaries of commercial fishing, water flow conditions in Bare Creek, and ocean environmental conditions. Notably, for several years during 1950–61, Bare Creek had such low flows that adults were prevented from reaching the lake; low flows may have also restricted smolt out-migrations (Table 7-4).

Considering the limitations of the Bare Lake system, it would seem unlikely that significant fertilization results would be observed beyond the changes in water chemistry, plankton, benthos, and young sockeye. In our view, Nelson's fertilization experiment at Bare Lake was remarkably successful because he found increased growth and survival of young sockeye salmon. After all, smolts are the end product of the freshwater phase of the sockeye's life cycle; the productivity and success of adults comes mainly from the marine phase, a period that can easily cancel any benefits received in the nursery lake.

In retrospect, several improvements to the Bare Lake experiment would have strengthened the results and answered some persistent questions about the effects of the fertilization. First, a concurrent study of a similar unfertilized control lake would have helped to separate the relative contributions of natural environmental changes from the artificial fertilizer additions. Second, at least a year of pre-fertilization baseline study of Bare Lake's limnology and biota was needed. Third, the abundance of all fish species that inhabited Bare Lake should have been determined prior to the fertilization, particularly for its sockeye and coho salmon, Dolly Varden, and threespine stickleback. Fourth, further information was needed on the foods of young sockeye, especially since they fed mainly on the benthos of Bare Lake and not on its zooplankton. Of course at the time, Nelson lacked the options of doing pre-fertilization studies, adding a control lake, or performing additional studies, because of limited funding, personnel, and time. Instead, he focused on the main components of the fertilization experiment—water chemistry, plankton, and sockeye salmon juveniles and adults. These topics alone comprised a full field program, with little time left for other fish or lake studies.[41] Further, considerable urgency existed within the FWS to begin the fertilization experiment at Bare Lake so the results could soon be applied to Karluk Lake.

Nelson realized that the Bare Lake study had some deficiencies and wanted to address them. In particular, he was concerned whether the results from Bare Lake

[41] Nelson, Philip R. Personal commun. with Richard L. Bottorff, 16 February 1998.

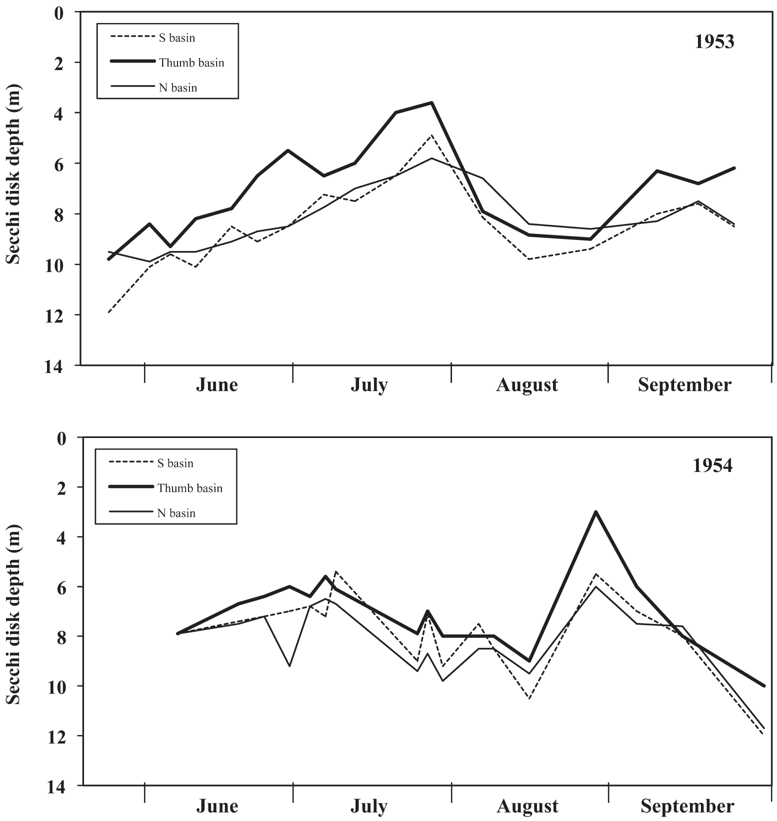


Figure 7-6. Seasonal variation of Secchi disk depths (m) in the three basins of Karluk Lake, 1953–54. From Bevan and Walker (1955).

could be applied to Karluk Lake; the two lakes had distinct physical, chemical, and biological differences. In 1955 Nelson proposed a second lake fertilization experiment on Kodiak Island, but this time he wanted to use a deep lake that thermally stratified in summer, as did Karluk Lake.[42] In a new field trial, 2–3 years of baseline studies would precede the fertilization and ongoing limnological studies at Karluk Lake would serve as an experimental control. His proposal was a worthy expansion of the Bare Lake study, but this second lake fertilization experiment was never done.

Although Nelson devoted much of his effort to the Bare Lake experiment during 1950–56, he also continued many research programs at Karluk Lake with the assistance of four to five temporary FWS biologists. Of course, Nelson's ability to do research at two separate lakes was only possible with regular support from several FWS amphibious aircraft. At Karluk Lake, the biologists regularly collected the standard limnological data every two weeks at three sampling stations, though little of this data was ever included in FWS reports.

Besides the federal employees at Karluk Lake during this period, several FRI biologists also worked there and at times assisted the FWS studies. FRI biologists Bevan and Walker independently collected limnological data to better understand the rearing environment of young sockeye in Karluk Lake. Initially during 1948–51, they simply measured water temperatures wherever they traveled at the lake, but during 1952–54 they expanded these studies to all three basins. In particular, every week they measured water temperature profiles with a bathythermograph and water transparencies with a Secchi disk (Bevan, 1953; Bevan and Walker, 1954, 1955). Their conscientious efforts resulted in some of the most detailed data ever collected on the seasonal variation of water transparencies in Karluk Lake. These transparencies had a distinct bimodal pattern because of regular changes in the fine particles and plankton suspended in the water column (Fig. 7-6). In August–September 1952, Bevan collected Karluk Lake's plankton with a Hardy sampler and analyzed them for a limnology course at the University of Washington. Common taxa of phytoplankton were *Chlamydomonas*

[42] Letter (8 November 1955) from Philip R. Nelson, Fishery Research Biologist, FWS, Seattle, WA, to Administrator, Alaska Commercial Fisheries. Located at NARA, Anchorage, AK.

Fisheries Research Institute biologist using a bathythermograph, Karluk Lake, 1952. (Charles E. Walker, Sechelt, BC)

Fisheries Research Institute biologist Bill Mulligan measuring water transparency with a Secchi disk, Karluk Lake, 1952. (Charles E. Walker, Sechelt, BC)

and *Tabellaria,* and of zooplankton were *Bosmina, Cyclops,* and *Daphnia.*[43] Bevan and Walker (1955) often measured the river's discharge with a current meter and related this flow to the lake's level, in effect deriving a discharge-rating curve for the Karluk system. They also collected climatological data, such as maximum and minimum daily air temperatures, daily surface water temperatures, precipitation, and sky conditions.

Bevan and Walker monitored the water level of Karluk Lake during 1950–54 and found that it fluctuated 50–80 cm during a full field season (Fig. 7-7). Typically, the water level increased each spring to a peak in early to mid June as snowmelt runoff entered the lake, followed by a gradual decline from mid June to early August. Depending upon the exact timing of autumn rainstorms, water levels again started to increase sometime between mid August and mid September. Although they did not measure winter water levels, the lake receded in this season.

This same seasonal bimodal pattern was also found by the U.S. Geological Survey during 1974–82 when they monitored the discharge of the Karluk River. Of course, in each year the seasonal pattern of lake water level differed somewhat from the norm, reflecting specific weather conditions. This was most obvious in 1954 when more than 100 mm of rain fell on the Karluk Lake watershed on 21–23 August. This extreme storm, which was even more violent at the south

[43] Bevan, Donald E. 1952. Karluk Lake plankton. Kodiak Island Research, FRI, University of Washington, Seattle, WA. Unpubl. report. Located at FRI Archives, University of Washington, Seattle, WA.

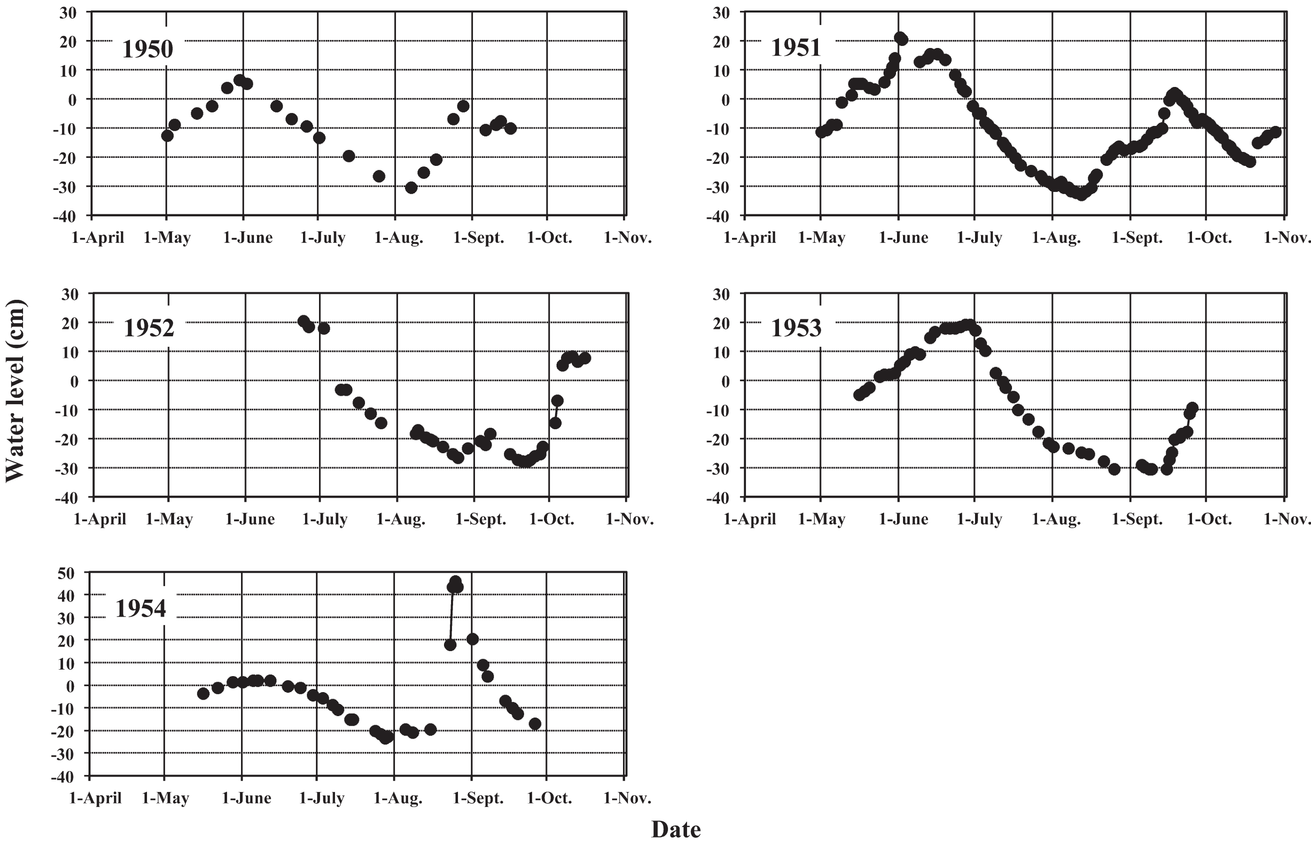


Figure 7-7. Water level of Karluk Lake, 1950–54. The data are from 1950–54 weather records, FRI Archives, University of Washington, Seattle. All graphs are plotted to the same scale, except for 1954.

end of the lake, caused widespread flooding, eroded many spawning tributaries, shifted stream channels, stranded sockeye eggs previously buried by spring-run sockeye, triggered landslides on steep mountain slopes adjacent to the lake, and increased the lake's water level about 60 cm within a couple of days (Bevan and Walker, 1955).[44]

In spite of their meticulous measurements of the lake's limnology and climate, Bevan and Walker viewed these accumulated facts as general background information, rather than as data to investigate specific questions about the lake and its young sockeye. In fact, in 1955 they declared that "at present we have no specific application for any of the measurements of physical factors" (Bevan and Walker, 1955).

[44] Meadow Creek was especially altered by the storm, as shown by the dramatic photographs in the report by Bevan and Walker (1955). They estimated that the flow of Meadow Creek increased over 100-fold and that there was nearly a complete loss of sockeye eggs. Other heavily impacted streams were Canyon, Halfway, Grassy Point, Cascade, and Upper Thumb.

1957–1962: Post-Fertilization Studies at Bare Lake and Limnological Studies at Karluk Lake

When Nelson ended the fertilization experiment at Bare Lake in June 1956, the impetus to continue the study and do additional enrichments declined. Although he urged the BCF to continue the annual fertilizations and suggested they control the Dolly Varden and stickleback populations in the lake, these recommendations were never followed.[45] The BCF remained interested in the Bare Lake results and the possibility of enriching Karluk Lake, but the failure to increase the number of returning adult sockeye, and other uncertainties with the study, caused the field work there to be gradually discontinued as new biologists pursued other research interests.

Nevertheless, post-fertilization studies of Bare Lake were done with varying degrees of intensity during

[45] Letter (11 June 1957) from [Phil Nelson], FWS, Annapolis, MD to John Owen, FWS, c/o Roy Lindsley, Kodiak, AK. Located at NARA, Anchorage, AK.

1957–61. For example, the zooplankton populations of Bare Lake were studied in 1957 (Raleigh, 1963) and the lake's fish populations were monitored during 1957–61, including the out-migrating sockeye smolts, returning sockeye adults, Dolly Varden, and coho salmon smolts (Table 7-4). The number of sockeye smolts appeared to decline after the last fertilization in 1956.

All post-fertilization studies ended at Bare Lake after the 1961 field season, and this date marked a temporary halt to Rich's 1926 idea that the influx of salmon-carcass nutrients helped to sustain sockeye production in Karluk Lake. This curtailment typifies the fate that often befalls explanations of complex scientific questions—competing theories gain or lose favor over time as new data are interpreted and alternative explanations are tested. Yet, for sockeye salmon systems in Alaska, the Bare Lake experiment was an important first step in understanding the connection between lake fertility and salmon production. Though biologists planned the Bare Lake study as a prelude to the fertilization of Karluk Lake, this was not accomplished for several more decades, until lake enrichment gradually became an accepted method for rehabilitating depleted salmon runs.

An intense debate developed within the BCF during 1957–62 about the value of fertilizing Karluk Lake to bolster its declining sockeye runs. Rounsefell, with the publication of his influential 1958 paper on Karluk's sockeye salmon, intensified the debate about the correct rehabilitation methods. Agency biologists and officials then actively read and discussed his paper. Rounsefell recommended that Karluk Lake be fertilized, but his statement lacked conviction, even though he had stated in 1952 "that smolt length is highly dependent on both temperature and number of carcasses".[46] And yet, by 1958 he found "no positive evidence to support the theory of declining fertility" in Karluk Lake and declared that any temporary fertilization benefits to young sockeye might soon be absorbed by increased numbers of predatory fishes. His prediction that lake enrichment was futile only further stimulated discussions on this topic, with strong arguments given on both sides. Eventually, the BCF decided not to fertilize Karluk Lake.

Rounsefell's ambivalence about the fertility of Karluk Lake caused some BCF biologists to pursue other topics of sockeye salmon research. John Owen, BCF research leader at Karluk in 1957, also discounted the fertility theory and believed that other causes best explained the decline in sockeye abundance:

> As far as the fundamental Karluk problem is concerned I am now inclined to think that the basic fertility theory may have less merit than the timing of the escapement also its size and apportionment to the various spawning grounds. Reading the old files almost convinces me that a decline in fertility was something seized upon as an explanation … at the end of a long period of research and management which had been disastrous to the run.[47]

In fact, Owen wanted the lake fertility studies moved to the salmon research project at Brooks Lake, Alaska, where other BCF biologists could pursue the idea. Since research funds and personnel were then limited at Karluk, such a transfer would let Owen focus on the relative productivities of different sockeye subpopulations and the qualities of their spawning habitats. A formal transfer of the fertility research was not done, and at least some lake studies continued at Karluk for the next decade, if only because of 30 years of inertia on the topic.

Collection of limnological data occurred irregularly at Karluk Lake during 1957–62. Only minimal data were collected in 1957, but Owen and his assistants then decided to resolve the lake fertility debate in 1958. Consequently, they did a detailed limnological study that year and compared their results with that done in 1927 (Conkle et al., 1959). In 1958 they examined Karluk, Thumb, and O'Malley lakes and several tributary creeks for many factors, including water temperature profiles, transparencies, pH, free and bound carbon dioxide, dissolved oxygen, nitrogen, phosphorus, silica, and plankton. Again, phosphorus concentrations in tributary streams were significantly higher downstream from decomposing salmon carcasses. But despite the new data, they found little evidence that chemical nutrients had declined since 1927, even though sockeye escapements and salmon carcasses were much lower in 1958. And unexpectedly, some nutrients apparently were greater in 1958. Based on the 1958 data, they discounted the theory that reduced lake fertility had limited the survival of young sockeye in Karluk Lake (Conkle et al., 1959):

> [Comparing 1927 and 1958 limnological conditions in Karluk Lake] If salmon carcasses contribute major amounts of inorganic salts to the lake, we would expect a corresponding drop in the inorganic salts content of the lake waters. This drop is not indicated. While the

[46] Rounsefell, George A., and Richard F. Shuman. 1952. Population dynamics of the sockeye salmon, *Oncorhynchus nerka*, of Karluk River, Alaska. FWS, Woods Hole, MA. Unpubl. report. 72 p. Located at ABL, Auke Bay, AK.

[47] Letter (30 September 1957) from John B. Owen, FWS, Karluk Lake, AK, to W. F. Royce, FWS, Juneau, AK. Located at NARA, Anchorage, AK.

> total phosphorus content of the lake may or may not have decreased, other chemical compounds tested show an increase in concentration. It may reasonably be deduced then that the concentrations of inorganic salts may fluctuate independently of the numbers of spawners entering the lake . . . At the present low level of abundance of sockeye smolts in Karluk Lake, lack of lake fertility does not appear to be a limiting factor in survival.

Significantly, the 1958 study affirmed the BCF's recent decision not to fertilize Karluk Lake, and no further limnological measurements were made at the lake in 1959–60, though this would only be a brief lapse.

In 1961–62, Karluk Lake was included as part of a large comparative investigation of many sockeye salmon lakes in southwestern Alaska (Burgner et al., 1969; Hartman and Burgner, 1972). For this regional study, a wide range of limnological data were collected at all of the study lakes, including water temperatures, transparencies, phytoplankton productivity and standing crop, and water chemistry (total dissolved solids, alkalinity, pH, dissolved oxygen, sodium, potassium, calcium, magnesium, manganese, iron, nitrate, and silica). For the first time, biologists measured the primary productivity of Karluk Lake by using carbon-14 methods and the phytoplankton standing crop by using chlorophyll-a. Karluk Lake had a similar water chemistry to other sockeye salmon lakes in southwestern Alaska, but had relatively high values of primary productivity and phytoplankton standing crop.

Although nearly all studies of Karluk Lake prior to 1956 were focused on its sockeye salmon, a few scientists conducted independent research there with nonfishery goals. For example, Douglas Hilliard, a parasitologist with the Arctic Health Research Center in Anchorage, Alaska, studied the plankton of Karluk Lake in 1956–57 to learn about the life cycle of the tapeworm *Diphyllobothrium ursi,* which infests brown bears. Larval stages of this parasite infest intermediate hosts such as sockeye salmon and planktonic copepods. To find the larval parasite in the copepods, he meticulously collected and identified the plankton of Karluk Lake throughout a full yearly cycle. In addition to the zooplankton, he studied the lake's phytoplankton and recorded 255 species and varieties, most of them being diatoms (Hilliard, 1959a).

Hilliard's work was especially insightful about Karluk Lake, being the first to report abundant plankton populations in late autumn and winter; previously they were thought to be sparse in those seasons. He found that diatom densities declined between July and September, just as Juday et al. (1932) had previously reported, but then the densities increased to a second peak in October. Likewise, densities of the macrozooplankter *Cyclops* were higher in October–December than during summer months. Using Hilliard's samples from Karluk Lake, Emile Manguin (1960) of the Muséum National d'Histoire Naturelle, Paris, France, analyzed its diatoms, prepared drawings and photographs of the species, and described 51 new taxa (Kociolek and de Reviers, 1996), while Hannah Croasdale (1958) of Dartmouth College studied its desmid algae.[48]

In 1957, George Eicher and Rounsefell published an interesting paper on the fertilizing effects of volcanic ash falls on lake productivity and salmon abundance in southwestern Alaska. This region has many active volcanoes that irregularly eject ash into the atmosphere; these particles eventually fall onto nearby watersheds that drain into sockeye salmon lakes, adding nutrients that increase lake productivity. Though they did not discuss this idea for Karluk Lake, it was, nevertheless, relevant to lakes on Kodiak Island since several volcanoes lie on the Alaska Peninsula only 80 km northwest across Shelikof Strait. Ash falls have reached the island many times within recorded history, the most notable in recent history being the 1912 eruption of Novarupta on the mainland. Field biologists at Karluk Lake often observed light ash falls during the 1920s–1950s. Archaeological excavations and sediment cores at and near Karluk Lake have documented that several significant ash falls have occurred over the last few thousand years (Nelson and Jordan, 1988; Knecht, 1995; Finney, 1998; Finney et al., 2002). Although the possibility of lake enrichment from volcanic ash is an intriguing idea, the true significance of this phenomenon on Karluk Lake's productivity and sockeye salmon remains unknown.

1963–1969: BCF Routine Limnological Sampling

The BCF regularly collected limnological samples in the north basin of Karluk Lake during 1963–69, including water temperature profiles, transparencies, pH, and alkalinity. They also operated recording thermographs for air and water temperatures at the Karluk River weir and

[48] Hilliard also studied the chrysophyte algae from Pinguicula Lake, a small lake tributary to the lower Karluk River (Hilliard, 1969). His colleague, Robert Rausch, collected the chrysophyte samples in 1962 as part of a larger study of the Kodiak Island Refugium (Karlstrom et al., 1969). The scientists doing these studies used the Bare Lake cabin and facilities as their base camp.

Grassy Point Creek (including the winter months). Climatological data such as air temperatures, precipitation, wind speeds, sky conditions, and solar radiation were monitored at the Karluk River weir or at Camp Island during this period. Despite these efforts, no limnological data were published in departmental reports or used in specific biological research during these years.[49]

1967–1978: Initial Limnological Studies of the ADFG

The ADFG became fully responsible for management of the state's salmon fisheries in 1960 and began research on Karluk's sockeye salmon soon thereafter. These studies, including a limnological survey of Kodiak Island lakes, received partial funding from the U.S. Anadromous Fish Act of 1967. Because of its important fisheries, Karluk Lake was one of the first lakes that the ADFG investigated; ADFG's long-term goal was to rehabilitate Karluk's sockeye salmon runs. Roger Blackett, ADFG fishery biologist, first collected limnological samples at Karluk, Thumb, and O'Malley lakes in 1967–68 (Blackett, 1968; Blackett and Eaton, 1968; Blackett et al., 1969) and prepared bathymetric maps for each lake.[50]

This initial work at Karluk led to the ADFG's decision in the early 1970s to restore the sockeye salmon run of the Upper Thumb River (Blackett et al., 1970; Blackett and Davis, 1971).[51] To accomplish this task, the biologists initially focused their sampling efforts on Thumb Lake since it served as rearing habitat for newly emerged sockeye fry before they migrated to Karluk Lake. The limnological data they collected—water temperature profiles, water chemistry (pH, carbon dioxide, dissolved oxygen, and alkalinity), and seasonal changes in zooplankton abundance and composition—were an essential part of preparing for and monitoring the rehabilitation project (Blackett, 1973). Thumb Lake, being shallow, developed little thermal stratification in summer and usually overturned in September. Phytoplankton abundance normally peaked in August, while zooplankton abundance peaked in August–September.

Following the work at Thumb Lake, the ADFG made detailed baseline studies of Karluk Lake's limnology in 1973–75 and 1978, as they continued with plans to restore the sockeye runs of the Upper Thumb River and several other lake tributaries.[52] These studies included measurement of the lake's water chemistry (pH, dissolved oxygen, specific conductance, and nitrogen, phosphorus, and silica nutrients). They found few chemical differences between the 1973–75 data and that of 1927, except for an unexplained large increase in nitrite and nitrate nitrogen. Significantly, they found that zooplankton densities in 1973–75 and 1978 were less, by nearly an order of magnitude, than those in 1927–30. Large reductions in zooplankton densities had also occurred in Thumb and O'Malley lakes.

Restoration of early-run sockeye of the Upper Thumb River began in earnest in 1978 and continued until 1986 under the leadership of ADFG fishery biologist Lorne White. The rehabilitation was accomplished by incubating and planting millions of eyed-eggs and fry into the river above Thumb Lake (White, 1988b). A streamside incubation facility was built and operated on the Upper Thumb River, and biologists implanted the eggs into the river's substrate with an innovative egg planting device. During this period, the zooplankton populations of Karluk, Thumb, and O'Malley lakes were monitored to assure that the limnetic food base would support the larger numbers of young sockeye (White, 1985, 1986, 1988a).[53] The total density of zooplankton in Karluk Lake fluctuated between a mean of 5,110 and 42,740 per m^3 during 1973–87; zooplankton composition varied between crustaceans (cladocera and copepods) and rotifers (Fig. 7-8). Both cladocera and

[49] Raw limnological data from 1963–1969 are present in station notebooks and data files. Located at NARA, Anchorage, AK.

[50] 1) Blackett, Roger F. 1970. Kodiak sockeye rehabilitation, project proposal and budget FY 71–72. ADFG, Kodiak (September 30,1970). Unpubl. report. 42 p. Located in FRED papers, ADFG Library, Douglas, AK.
2) White, Lorne E. 1976. Karluk sockeye restoration. Project Brief. ADFG, FRED (December, 1976). Unpubl. report. 68 p. Located at ADFG Office Files, Kodiak, AK.

[51] See footnote 50 (Blackett, 1970).

[52] See footnote 50 (White, 1976).

[53] Also see the four unpublished reports by Lorne E. White, as follows:
1) White, Lorne E. 1976. Karluk sockeye restoration. Project Brief. ADFG, FRED (December, 1976). Unpubl. report. 68 p. Located at ADFG Office Files, Kodiak, AK.
2) White, Lorne E. 1978. Karluk Lake sockeye rehabilitation, 1978. Operational Plans. ADFG, FRED (January, 1978). Unpubl. report. 62 p. Located at ADFG Library, Douglas, AK.
3) White, Lorne E. 1979. Karluk Lake sockeye rehabilitation. Project Proposal, 1980–1981. ADFG, FRED (December, 1979). Unpubl. report. 57 p. Copy in personal papers of Richard Gard, Juneau, AK.
4) White, Lorne E. 1985. Karluk Lake sockeye rehabilitation, 1978–1984. ADFG, FRED, Juneau (March, 1985). Unpubl. report. 45 p. Located at ADFG Office Files, Kodiak, AK.

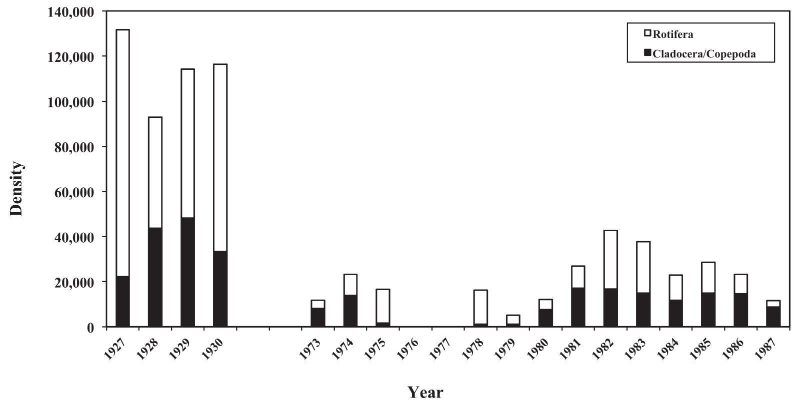


Figure 7-8. Mean annual density (number/m^3) and composition of zooplankton in the three basins of Karluk Lake, 1927–30 and 1973–87. The 1927–30 data are from Juday et al. (1932) and the 1973–87 data are from White (1988a). All plankton were collected from the upper 35–50 m of each basin, except for the south basin (0–125 m) during 1927–30. The 1927–1930 raw data were reduced by 50% to better match modern plankton analyses. Copepod densities from both eras included the mature forms and nauplii larvae.

copepods were major foods of young sockeye, while rotifers were little used. Compared with the plankton densities recorded during 1927–30 (Juday et al., 1932), substantially fewer crustaceans and rotifers occurred during 1973–87, and this indicated that Karluk Lake's fertility had decreased over the intervening 50 years.[54]

Until the ADFG began its studies of Karluk Lake in the 1970s, little was known about the lake's limnology in winter because nearly all previous sampling had been done between April and October. To our knowledge, only one fisheries biologist ever over-wintered at Karluk Lake, ADFG biologist Peter Rob, who spent three winters (1976–1979) at the lake collecting data on stream flow, water chemistry, and salmon spawning habitats.[55]

1979–1990: Resurgence of the Salmon-Carcass Nutrient Idea and Fertilization of Karluk Lake

The management, conservation, and enhancement of Alaska's salmon resources underwent considerable change during the 1970s as the Alaska State Legislature created new agencies and expanded the powers of the ADFG. For example, they created the Division of Fisheries Rehabilitation, Enhancement, and Development (FRED) within the ADFG in 1971, followed by the Commercial Fisheries Limited Entry Commission in 1972 and Private Nonprofit Hatchery Program in 1974. The Legislature allowed for Regional Aquaculture Associations in 1976 and directed the ADFG Commissioner to develop comprehensive regional salmon plans.

Rehabilitation of the sockeye salmon run in the Upper Thumb River was an early project of the ADFG and its new FRED Division, which also developed many ideas for the enhancement of Alaska's salmon resources, including fisheries regulations, hatcheries, stream restorations, fish barrier removal, predator control, lake fertil-

[54] The plankton data of 1927–30 and 1973–87 may not be entirely comparable because each study used different sampling protocols, plankton nets, and analyses, but we have attempted (possibly incorrectly) to make them equivalent. First, the plankton nets of each study differed in dimensions and mesh size. Juday et al. (1932) used a net with a 12 cm diameter opening and # 20 bolting silk (aperture opening = 76 µm), while White (1988a) used a net with a 30 cm diameter opening and a mesh opening of 130 µm. These mesh-size differences alone would tend to make Juday's plankton densities higher than White's plankton densities. Second, Juday's data were average plankton densities obtained for hauls from the lake bottom to surface, this distance differing by lake basin—south basin (0–125 m), Thumb basin (0–45 m), and north basin (0–50 m)—while White's data were average plankton densities from the upper 35–50 m of the three basins. Since plankton densities are often higher in the upper water layers, sample depth alone would tend to make Juday's results less than White's results. That is, if Juday had just included the upper 50 m in his analysis, the densities of cladocera and copepods he reported would have been much higher. Third, Juday multiplied the plankton counts by 2 to account for the fact that his net only retained one half of the plankton in the water column, while modern protocol apparently does not make this correction. Thus, to standardize the results, we divided Juday's data by 2. Without this correction, the differences in plankton density between the two periods become even more dramatic, with crustaceans and rotifers in the early years being much more abundant than in 1973–1987. Fourth, some uncertainty exists about which zooplankton groups were included in the two studies. We have included in Fig. 7-8 the cladocera, copepods, copepod nauplii, and rotifers for 1927–30 because it appears that all of these zooplankton groups were included in the 1973–87 data (See White, Lorne E. 1976. Karluk sockeye restoration. Project Brief. ADFG, FRED (December, 1976). Unpubl. report. 68 p. Located at ADFG Office Files, Kodiak, AK). In summary, the first two study differences tend to counteract each other, while the third and fourth differences have been adjusted for. Juday (1916) provides a full description of the closing plankton net they used at Karluk Lake.

[55] Peter Rob's winter observations at Karluk Lake are unique, but the present location of his data and field notebooks are unknown.

izations, and others. To pursue such improvements, it soon became apparent that the ADFG needed personnel with scientific expertise in limnology. Knowledge of lakes and their ability to produce juvenile sockeye salmon was important when determining the stocking rates of eggs and fry in freshwaters and planning lake fertilization projects. Thus, the ADFG Limnology Laboratory, with its central facility located in Soldotna, Alaska, was created in 1979 within the FRED Division. Several limnologists were hired to organize the new laboratory, collect field data, conduct research, and design rehabilitation projects. FRED had already started to rehabilitate the sockeye run in the Upper Thumb River when the limnology laboratory was created, but this new unit quickly proved to be beneficial. Limnologists collected and analyzed lake samples and provided information on the lake's ability to supply zooplankton food for greater numbers of juvenile sockeye.

Ever since the Limnology Laboratory was created in 1979, limnological data has been regularly collected each year at Karluk Lake using standardized methods and modern analytical equipment (Koenings et al., 1987; Schrof et al., 2000; Schrof and Honnold, 2003). Samples were taken every 4–6 weeks from May through October and analyzed for a wide range of physical, chemical, and biological factors, including water temperature profiles, transparencies, solar radiation profiles, dissolved oxygen profiles, specific conductance, pH, alkalinity, turbidity, color, calcium, magnesium, iron, phosphorus, nitrogen, silicon, organic carbon, chlorophyll-a, phaeophytin-a, phytoplankton density and species composition, and zooplankton density and species composition.[56] On a less regular basis, lake samples were collected during late autumn and winter.

Limnological data collected at Karluk Lake in the late 1970s and early 1980s had a purpose beyond monitoring the rehabilitation project at the Upper Thumb River—they were an important baseline of information for planning the artificial fertilization of the lake. During this period, several fishery agencies along the Pacific Coast were testing the lake fertilization idea to see if salmon populations could be enhanced. Likewise, limnologists at the ADFG began exploring the feasibility of enriching Karluk Lake to increase sockeye abundance and reexamined the possibility that long-term reductions in lake fertility had depleted these runs and prevented their recovery. Certainly, the commercial fishery had annually harvested large numbers of adult sockeye that otherwise would have reached Karluk Lake and added their nutrients to the lake (especially phosphorus and nitrogen) when carcasses decomposed. It was reasoned that the nutrients transported upstream in the bodies of adult salmon eventually entered the lake and stimulated phytoplankton growth, the primary trophic base that supported the zooplankton eaten by juvenile sockeye.

In planning for the fertilization of Karluk Lake, the ADFG limnologists reviewed past studies of the lake's water chemistry and fertility and the Bare Lake experiment (Juday et al., 1932; Barnaby, 1944; Nelson and Edmondson, 1955; Rounsefell, 1958; Nelson, 1958, 1959). They examined Rounsefell's paper because he claimed that lake fertility had not declined as the sockeye runs decreased. Significantly, several errors or incorrect assumptions were discovered in his analysis of the quantity of phosphorus stored in Karluk Lake and the annual influx of this element coming from salmon carcasses and watershed sources (Koenings and Burkett, 1987b). After correcting for these errors, it was obvious that salmon carcasses were a major source of phosphorus to Karluk Lake each year. For example, an escapement of 1,000,000 adult sockeye salmon provided 8,074 kg of phosphorus to the lake, while annual tributary inflows from the surrounding watershed supplied 5,622 kg. Thus, collection of the baseline limnological data during 1979–86 and review of the literature convinced the ADFG that fertilizing Karluk Lake would benefit its sockeye salmon. They proceeded with the enrichment.

The scientific rationale for the fertilization project was given by the ADFG limnologists Jeffery Koenings and Robert Burkett (1987a, b), their analysis documenting that Karluk Lake's fertility had declined between the 1920s and 1980s. This reduction was evident in the phosphorus levels of Karluk Lake and several lateral streams; the peak phosphorus concentrations in the spawning creeks were directly related to sockeye escapements. Notably, they discovered that phosphorus levels varied seasonally, being low in June–July and then rapidly increasing in August–October, as salmon carcasses decomposed. Undoubtedly, these nutrient pulses caused seasonal variations in the lake's macrozooplankton, which were more abundant in September–November than in May–August. In contrast, the concentrations of reactive silicon, not an ingredient supplied by salmon carcasses, had little seasonal or yearly variation in the lateral streams. Lower lake fertility also had affected the sockeye salmon smolts during this 60-year period by reducing their total numbers (by

[56] This large database is stored on computer files at the ADFG Limnology Laboratory, Soldotna (now known as the ADFG Region II, Central Regional Limnology unit), and at the Kodiak office.

nearly 80%), total biomass (by nearly 90%), and mean lengths and weights (by 40%), but not their age structure. The diminished smolts suggested that an equivalent reduction had occurred in the sockeye salmon fry. Koenings and Burkett (1987b) estimated that Karluk Lake had an annual rearing limitation of 18,000,000 sockeye smolts, well above the actual production since the 1920s. They found that the sockeye fry density was below the lake's carrying capacity.

Since much of Karluk Lake and its watershed lies within the Kodiak National Wildlife Refuge, USFWS managers and biologists were keenly interested in the nutrient-addition program of the ADFG. Thus, when planning began in the early 1980s to fertilize Karluk Lake, refuge managers requested technical assistance from USFWS fishery biologists to evaluate the idea. In 1982 the ADFG and USFWS signed a formal agreement to cooperate in restoring the sockeye salmon of Karluk Lake, with the goal to increase annual escapements to 800,000–1,000,000 fish. For their part of the agreement, USFWS biologists conducted research at Karluk Lake during 1982–88, testing several theories of what had caused the previous decline in sockeye abundance. Their studies focused on five topics: distribution and abundance of lake resident fishes, competition between juvenile sockeye and threespine sticklebacks, charr predation on juvenile sockeye, genetics of different components of the adult sockeye run, and historical lake fertility as revealed in sediment cores.[57]

Of the five investigations, the sediment core work done by USFWS biologist Terry Terrell was an innovative attempt to resolve just how important salmon-carcass nutrients were to lake fertility and salmon production in the Karluk ecosystem.[58] In this study, she collected several core samples from the bottom sediments of Karluk Lake in 1981 and another four in 1982 (two from the north basin and two from the Thumb basin). The sediments were largely accumulations of the silica valves of diatoms that had settled to the bottom from the lake's phytoplankton. Radiocarbon dating showed that the sediments extended back at least 1,000 years.

Terrell inspected the cores for two types of diatoms, araphidneae and centric, the ratio of these two kinds being a gauge of past trophic conditions in Karluk Lake (i.e., oligotrophic, mesotrophic, or eutrophic). Although her results had uncertainties, the lake's fertility (usually mesotrophic) had experienced large changes over time, fluctuating between oligotrophy and eutrophy. Further, the diatom ratios varied in distinct cycles, one of 10–15 years and another of 55–75 years. Terrell also noticed variations in the abundance of cladoceran body parts and *Chara* oogonia.

Regrettably, precise correlations between diatom ratios and sockeye escapements were impossible in this study because of problems in accurately dating the sediment layers. Terrell (1987) recorded 98 taxa of diatoms in the sediment cores and compared her list with earlier studies of Karluk Lake (Juday et al., 1932; Hilliard, 1959a; Manguin, 1960). Although her study failed to link lake fertility with sockeye escapements, it nevertheless showed that wide variations in fertility had occurred in the past and that sockeye-carcass nutrients remained a highly possible cause. In any event, showing that the lake's fertility had experienced substantial fluctuations prior to the commencement of commercial fishing was a notable accomplishment.

In early 1986, biologists of the USFWS and ADFG prepared an Environmental Impact Assessment for the proposed fertilization of Karluk Lake.[59] This report considered seven alternative fertilization plans; each had different combinations of the lake's three basins receiving nitrogen and phosphorus additions. Two alternatives evaluated the possibility of increasing nutrient inflows by letting two million pink salmon enter the lake, the enrichment would then come from natural decomposition of these salmon carcasses. The ADFG originally planned to add inorganic fertilizers to all three basins of Karluk Lake, but the preferred alter-

[57] USFWS biologists involved in these studies included Richard L. Wilmot, John D. McIntyre, Carl V. Burger, Terry T. Terrell, James E. Finn, Robert A. Olson, and Reginald R. Reisenbichler.

[58] Terry Terrell prepared at least two unpublished manuscripts on her sediment core studies.

1) Terrell, Terry T. 1982. Some observations on the trophic history of Karluk Lake. USFWS, Seattle. Unpubl. report. 18 p. Location of report unknown.

2) Terrell, Terry T. 1983. No title. USFWS, Seattle. Unpubl. report. 10 p. Copy from Terry Terrell, USFWS, Denver, CO.

[59] USFWS. 1986. The controlled addition of inorganic nitrogen and phosphorus into Karluk Lake. USFWS, Kodiak National Wildlife Refuge, Draft Environmental Assessment. Unpubl. report. 65 p. Located at USFWS Files, Kodiak National Wildlife Refuge, Kodiak, AK, and at ADFG Files, Soldotna, AK. The biologists directly involved in this report were Tony Chatto, Fishery Biologist, USFWS Kodiak National Wildlife Refuge, Kodiak, AK; Jeffery P. Koenings, Principal Limnologist, ADFG, Soldotna, AK; Kevin Ryan, Assistant Refuge Manager, USFWS Kodiak National Wildlife Refuge; and Richard L. Wilmot, Supervisory Fishery Biologist, USFWS, Alaska Fish and Wildlife Office of Research, Anchorage, AK.

native in the Environmental Impact Assessment was to fertilize only the main basin north of Camp Island and that was done.

The ADFG annually added inorganic nitrogen and phosphorus fertilizers to Karluk Lake from 1986 to 1990. They applied the liquid fertilizer in a fine mist sprayed onto the lake's surface by an aircraft that flew transects over the 5 km^2 application area, which was located where the three basins met north of Camp Island (Koenings and Burkett, 1988). In 1986 the fertilizer (87,272 kg of 27N–7P–0K) was added on 8 June–5 August, while in 1987 the same amount was added on 14 May–6 July. Koenings and Burkett (1988) summarized the results of the first two years of lake fertilization and were encouraged that sockeye salmon benefited from the treatment:

> [Concerning the 1986–1987 fertilization of Karluk Lake] Overall, the results achieved after enrichment at Station 3 are consistent with the broader concept that consecutive larger escapements can directly increase the next spring's rearing potential by recharging the system with marine nutrients. That is, our preliminary conclusion is that the nutrient enrichment at Station 3 has contributed to the increased production of herbivorous zooplankters during the early-spring period.

In the following years, fertilizer additions varied in the amounts and nutrient proportions (nitrogen-phosphorus-potassium): 87,272 kg of (27-7-0) in 1988, 77,272 kg of (20-5-0) in 1989, and 27,272 kg of (20-5-0) and 59,091 kg of (32-0-0) in 1990 (Schrof et al., 2000). Much of the funding for this fertilization project came from the Kodiak Regional Aquaculture Association and Kodiak Island Borough.

While the full results of the 1986–90 fertilization of Karluk Lake have yet to be analyzed and published, the ultimate effects on sockeye abundance may have been positive. Compared with the previous 30 years, sockeye salmon runs at Karluk were significantly larger during the fertilization and post-fertilization years (Figs. 1-2, 1-3). Escapements exceeded 1,000,000 fish in 1989 and 1991, the only years that this had happened since 1938.[60]

These encouraging results, however, were tempered by the fact that the abundance of sockeye and other salmon species also increased during this period throughout the Kodiak Island region, even in unfertilized lakes. Nevertheless, whether the larger populations of sockeye salmon came from natural causes or fertilizer additions, escapements to Karluk Lake substantially increased after 1985 and these fish greatly enhanced the annual input of salmon-carcass nutrients. It remains to be seen if these larger escapements and nutrient inputs will sustain the young sockeye and future abundant runs of returning adults. In any event, the present conditions are unique for testing the idea that production of sockeye salmon is linked with the influx of salmon-carcass nutrients to Karluk Lake.

1990–1998: Post-Fertilization Studies of Karluk Lake

Following the final fertilization of Karluk Lake in 1990, the ADFG Limnology Laboratory in Soldotna continued each year to monitor the standard set of limnological data until 2000; more recently the lake samples have been processed by the ADFG Near Island Laboratory in Kodiak.[61] Because regular samples have been gathered since 1980, a detailed and reliable database exists on the physical, chemical, and biological properties of Karluk Lake (Schrof et al., 2000; Schrof and Honnold, 2003).[62] Biologists also have monitored the variations of those zooplankton taxa most likely to be important food items for young sockeye; they are the crustacean macrozooplankters *Bosmina, Dapnia, Cyclops,* and *Diaptomus* (Fig. 7-9).[63] Of these four taxa, the copepod *Cyclops* consistently had the highest density and biomass, often by a factor of 10, while the cladocerans *Bosmina* and *Daphnia* and the copepod *Diaptomus* typically had similar lower abundances.

In the mid 1990s, the ADFG completed a new analysis of the sockeye salmon runs at Karluk to establish

[60] The 1989 escapement to Karluk Lake was larger than normal because the *Exxon Valdez* oil spill halted all commercial fishing that year, allowing the full sockeye run to reach the lake

[61] Much of the funding for the limnological monitoring of Karluk Lake comes from the Kodiak Regional Aquaculture Association. The ADFG Limnology Laboratory in Soldotna is now known as the ADFG Region II, Central Regional Limnology unit.

[62] Schrof et al. (2000) summarizes some of the limnological data for Karluk Lake through the mid or late 1990s. The full set of limnological data since the early 1980s exists on ADFG computer files.

[63] Since at least 1987, the ADFG plankton sampling protocol for Karluk Lake has been standardized (Koenings et al., 1987). Plankton samples were taken from the upper 50 m of the north and south basin and the upper 35–40 m of the Thumb basin using a net with a 20 cm diameter opening and a mesh opening of 153 µm. When plankton densities were low, a 50 cm diameter net was used. The 153 µm net was sufficient for capturing the sizes of macrozooplankton eaten by sockeye young, this data being of more interest to biologists than the smaller-sized plankton.

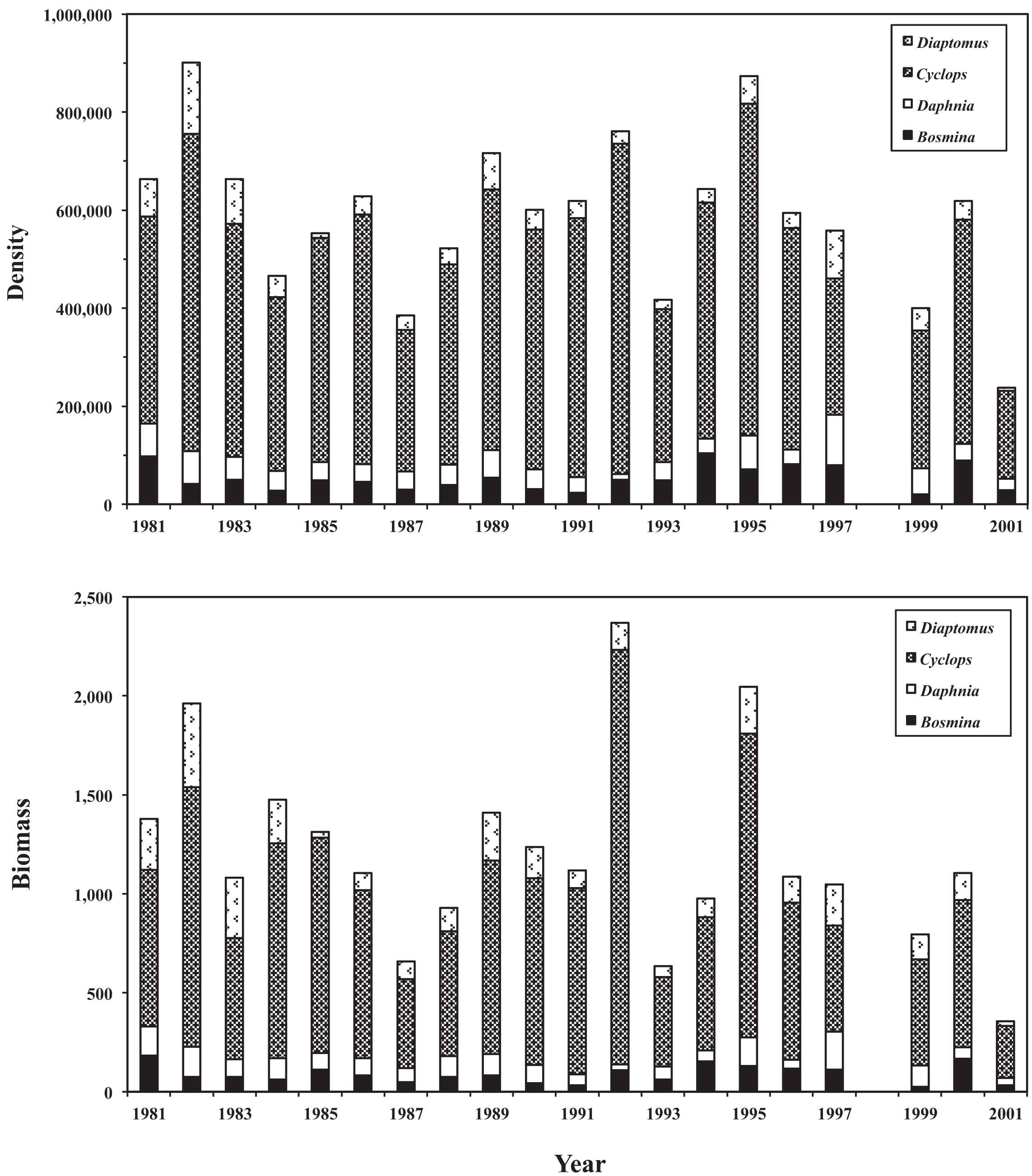


Figure 7-9. Macrozooplankton mean density (number/m²) and biomass (mg/m²) in the upper 50 m of the north and south basins of Karluk Lake, 1981–97 and 1999–2001. Data from Schrof and Honnold (2003). Copepod densities do not include the nauplii larvae.

an escapement goal that achieves maximum sustained yield (Schmidt et al., 1997, 1998). The comprehensive database on Karluk Lake (1980–94) and its adult sockeye salmon (1921–94) made it possible to analyze past runs using traditional spawner-recruitment models and also methods that incorporated limnological data. Significantly, the 65 years of sockeye data had three distinct levels of abundance—a period of relatively high production in 1922–45, a period of low production in 1946–78, and a recovery period in 1979–88. Ideally, the analysis would have included the early years of the fishery (1882–1920) since historic harvest records suggested that system productivity may have been even higher than during 1922–45 (Fig. 1-2). However, the early fishery era lacked relevant data on sockeye escapements, age compositions, and Karluk Lake limnology, and some uncertainty existed about the accuracy of early catch data.

By examining the limnological data, Schmidt et al. (1997, 1998) documented some key aspects of ecosystem function at Karluk Lake, the most significant being that the annual influx of salmon-carcass nutrients was vital to the long-term productivity of the lake. In particular, salmon carcasses supplied a substantial proportion of the annual phosphorus loading to the lake. Phosphorus was an important nutrient to algal production. Total phosphorus levels in July–August were directly related to the previous year's escapement (plus the fertilizer additions during 1986–90), and phytoplankton standing crops, as measured by chlorophyll-a, were directly related to total phosphorus concentrations.

At the next trophic level, zooplankton grazer biomass was inversely related to phytoplankton abundance, demonstrating that herbivores exerted a strong influence on phytoplankton abundance. Thus, primary production in Karluk Lake was controlled by nutrient levels and zooplankton grazers. Although phytoplankton levels must have strongly influenced the herbivore populations, a negative relationship between zooplankton grazer biomass and juvenile sockeye abundance (using escapement as a proxy) suggested that fish predation also exerted at least some control on the herbivores. The nature of the control was shown by inverse relationships between copepod biomass and early-run sockeye escapements of the previous year and between cladoceran biomass and late-run escapements of the previous year. These interactions indicated that seasonal feeding differences existed between early-emerging sockeye fry that mainly used the spring copepod bloom, while late-emerging fry mainly used the late summer cladoceran bloom. Further, the recruitment rate of early-run sockeye was positively related to cladoceran and copepod biomass, but this relationship was much weaker for late-run sockeye.

Schmidt et al. (1997, 1998) felt that sockeye salmon lakes such as Karluk, which depend upon regular inflows of salmon-carcass nutrients to sustain its high productivity, were rather rare. The limnological data from Karluk Lake showed that the long-term decline in sockeye spawners had reduced the inflow of nutrients to the lake and lowered its fertility, a process known as oligotrophication. The removal of sockeye salmon by the fishery apparently was aggravated in the 1960s and early 1970s by adverse ocean climates that further reduced the number of returning adults, though ocean conditions began to improve by the mid 1970s and partially aided the subsequent recovery of sockeye abundance. Starting in 1985, much higher escapements began to add substantial amounts of salmon-carcass nutrients to the lake, reversing the long-term decline in fertility and system productivity. Schmidt et al. (1998) believed that a positive feedback mechanism operated for Karluk's sockeye salmon whereby future runs were highly dependent on the nutrient benefits delivered by present escapements. They concluded that "the only consistent explanation of both long- and short-term trends in the recruitment data is found in nutrient loading of Karluk Lake from sockeye salmon carcasses."

Based on this new analysis, Schmidt et al. (1997, 1998) recommended an annual escapement goal of 800,000–1,000,000 sockeye salmon at Karluk, these being equally apportioned between the early and late runs. This fixed escapement goal had significant merits over a fixed harvest rate (or quota) for management of sockeye salmon. Because escapements affected the lake's fertility and forage base of juvenile sockeye, limnological data were crucial in setting this escapement goal. They cautioned that high escapements should be maintained to prevent future declines at Karluk, but if sufficient salmon-carcass nutrients could not be obtained from returning spawners, additional fertilizations of Karluk Lake might be needed.

1990–1998: Isotopic Analysis of Marine-Derived Nitrogen in Sockeye Salmon

Concurrent with the limnological studies and fertilization of Karluk Lake by the ADFG in the late 1980s and early 1990s, scientists from several educational institutions began to investigate the flow of nutrients, especially nitrogen, in the freshwater ecosystems used by sockeye salmon (Kline, 1991, 1992, 1993, 2003; Kline and Goering, 1993; Kline et al., 1990, 1993, 1997). In particular, they measured the proportion of the stable nitrogen isotope (^{15}N) present at different links of the food web that led to juvenile sockeye. Fundamental to this research is the fact that nearly all of the body mass of adult sockeye salmon is assembled from marine-derived components, which are enriched in ^{15}N over those that originate in freshwater. Consequently, when adult sockeye salmon return to their natal site to spawn, they transport marine-derived nutrients upstream and release them into the freshwaters when their carcasses decompose. These nutrients are next incorporated into the tissues of the freshwater biota, first into microorganisms such as algae and then via the food chain into zooplankton and young sockeye. By examining the stable nitrogen isotopes in the tissues of juvenile sockeye,

the proportions derived from marine and freshwater sources can be determined.

Isotopic analyses clearly demonstrated the importance of salmon-carcass nutrients to the growth of young sockeye at Karluk Lake. For example, most of the nitrogen (71–91%) in the body tissues of young sockeye was marine-derived and the proportion present was directly related to adult escapements (Kline, 1992; Kline et al., 1993, 1997). These results indicated, in contrast to many other Alaskan lakes, that young sockeye at Karluk were highly dependent on the marine-derived nutrients annually transported to the lake in the bodies of adult salmon. During 1986–92, a period of enhanced escapements to Karluk Lake, marine-derived nitrogen steadily increased in the zooplankton, sockeye fry, and sockeye smolts as the lake's fertility recovered from the low levels of the previous 30 years (Kline, 2003). Fertility was boosted by the large escapement of 1989 when commercial fishing was halted because of the *Exxon Valdez* oil spill.

Notably, the food chain that leads to sockeye salmon smolts at Karluk Lake was longer than for other Alaskan lakes, suggesting that more than the three typical trophic levels—phytoplankton, zooplankton, and young sockeye—were present. Additional trophic levels may have existed between herbivorous and carnivorous zooplankton or between age classes of juvenile sockeye, though these interactions remain unclear. Unexpectedly, isotopic analyses of the body tissues of sockeye pre-smolt juveniles and smolts indicated substantial feeding differences between these two life stages (Kline, 1993; Kline and Goering, 1993; Kline, 2003). Pre-smolt diets potentially changed from the typical zooplankton foods of summer to cannibalism on smaller sockeye juveniles or eggs (or predation on sticklebacks) in the autumn and winter just prior to their spring migration to the ocean. During this dietary shift, pre-smolt juveniles greatly increased in size (Kline, 1993). While these unusual results remain tentative, they emphasize the need to understand all life stages of young sockeye and all trophic level relationships, a task far from complete. The reasons for the exceptionally large smolts produced by Karluk Lake have always been a mystery to fishery biologists; a pre-smolt dietary shift toward cannibalism is a possible answer.

Little field evidence exists of cannibalism by young sockeye at Karluk or other Alaskan lakes, possibly because the dietary change occurs late in the year when ice-cover makes these fish inaccessible to normal sampling methods. Though only limited data are available on the food habits of juvenile sockeye at Karluk, cannibalism (or predation on sticklebacks) does not appear to be prevalent in summer, though a few records do exist. For example, when Fassett inspected the sockeye hatchery at Karluk Lagoon in August 1900, he stated that the larger sockeye fry were separated from the younger sac fry because of the "cannibalistic tendencies of the larger fry" (Moser, 1902). Barnaby, upon visiting Afognak Island hatchery on 18 May 1932, observed predation and cannibalism on newly released sockeye fry in the stream below the hatchery and declared that "all the fish reds and silvers in front of the raceway were eating the red fry which had been turned out at this spot.[64] Walker collected many juvenile sockeye at Karluk Lake in the summer of 1953 and occasionally noted cannibalism. He stated that "coho fingerling, and to a less extent, red fingerling have been found to contain small reds.[65] Rounsefell (1958) discussed the possibility that intra-specific competition in the form of cannibalism may occur in the juvenile sockeye of Karluk Lake:

> [Quoting Ricker about Fraser River sockeye salmon] Although the great bulk of sockeye food is plankton, there is a good possibility that these older sockeye, particularly after they have lived for two growing seasons, can consume young sockeye fry of later cycles. This has not yet been observed, but residual sockeye of 2 years of age have been found to eat young fish of other species, so there is little reason to doubt that they can consume sockeye fry.
>
> [Speaking of Karluk Lake sockeye salmon] The young sockeye migrating from Karluk Lake average very much larger, and older, than those of Cultus Lake, so there is an even greater probability that the older groups of young consume large quantities of the fry. The existence of such a relationship may help to explain how the dominant cycle year can occasionally fall very low . . . Recommendation 3 might not have to be carried out if predators are strictly controlled, but this is uncertain because the data available do not give sufficiently clear indications of the relative importance of predators and intraspecific competition (possibly cannibalism). This is a point on which research is sorely needed.

Besides the possible cannibalism, juvenile sockeye also occasionally preyed on sticklebacks at Karluk and Bare Lakes (Greenbank and Nelson, 1959):

> [Karluk & Bare Lakes, 1948–1956] Juvenile red salmon have been found with sticklebacks in their mouths or stomachs, but the act of capture has not been observed . . . The feeding habits of the young red

[64] See footnote 20.

[65] Walker, Charles E. 1954. Karluk young fish study, 1950–1954. Kodiak Island Research, FRI, University of Washington, Seattle, WA. Unpubl. report. Located at FRI Archives, University of Washington, Seattle, WA.

salmon in Karluk Lake are not fully known. It is probable that the fry eat insects and plankton animals, but the larger juveniles may eat a few small fish . . . As we have suggested above, small sticklebacks may be an item in the food supply of the salmon fingerlings, especially the larger smolts.

During a winter visit to Bare Lake in February 1955, Nelson caught many young sockeye by fishing through the ice with hook-and-line using salmon eggs as bait; this indicated that these fish had a wider diet than previously thought.[66] In 1956 Raleigh found stickleback and salmonid remains in the stomach contents of a few juvenile sockeye at Bare Lake:

[Bare Lake, 15 August 1956] A zero year class stickleback was found in the mouth of a dead red fingerling in the trap today.

[Bare Lake, 1956] A single sample of red salmon juveniles was analyzed for stomach food content. The analysis was of only the macroscopic organisms. A rough grouping of the results expressed as a volume percentage is as follows: diptera 40%; debris 35%; fish remains (sticklebacks and salmonidae) 10%; coleoptera 7%; trichoptera 5%; terrestrial insects 2%; plecoptera 1%.[67]

In summary, the above field observations suggest the possibility of cannibalism in juvenile sockeye but these few notes do not conclusively prove that it is a significant phenomenon at Karluk Lake, since some of this anecdotal evidence came from fish that were unnaturally confined in hatcheries, seines, and traps.

Because Karluk Lake is renowned for producing some of the largest sockeye salmon smolts in Alaska, one might expect that all early life stages of this species have been thoroughly studied in this system. Nevertheless, little knowledge exists about the food habits of Karluk's young sockeye, despite the paramount importance of the topic. Throughout Karluk's research history, biologists collected at least a few young sockeye to examine their foods, but most of this information was never formally published or presented in agency reports. Further, the little that is known about these diets was determined in summer, and nothing is known about winter and early spring foods. We believe that the lack of food habits information for juvenile sockeye is one of the most serious research omissions at Karluk.

[66] See footnote 40.

[67] 1) Raleigh, Robert F. 1956 notebook. Located at NARA, Anchorage, AK.
2) Raleigh, Robert F. 1956. Kodiak Island red salmon investigations, 1956 field season report. USFWS (December 31, 1956). Unpubl. report. 16 p. Located at ABL Office Files, Auke Bay, AK.

1994–2004: Paleolimnology—Isotopic Analysis of Marine-Derived Nitrogen in Lake Sediment Cores

Closely following the isotopic studies of juvenile sockeye tissues and lake food webs, the stable nitrogen isotope (^{15}N) was investigated in two sediment cores taken from the bottom of Karluk Lake in 1994 and 1995. The cores contained a 500-year record of marine-derived nitrogen; this nutrient was used as a proxy to reconstruct past sockeye salmon escapements (Finney, 1998). To calibrate the relationship between sockeye escapement and marine-derived nitrogen in the sediments, these data were first compared for the 1921–94 period, when escapements to Karluk Lake were accurately known. Indeed, a remarkably close correlation existed between known sockeye escapements and marine-derived nitrogen in the sediments. Significantly, this meant that the lake sediments contained a full record of past sockeye escapements. Analysis of the sediment profile would let biologists, for the first time, examine natural variations in sockeye salmon abundance centuries before the runs had been heavily exploited by commercial fishing.

Over the past 500 years, the sediment record showed that sockeye escapements to Karluk Lake varied widely in 50–100 year cycles, very similar to Terrell's previous results using diatom ratios.[68] The sediments also revealed that just as commercial fishing began at Karluk in the late 1800s, the sockeye runs were at peak abundance, and somewhat smaller runs were more typical for most of the pre-fishery years. In fact, pre-fishery escapements had averaged about 1,000,000 fish annually (range, 300,000–2,000,000) over the 500-year record. One million salmon carcasses would add 64,100 kg of nitrogen to the lake, while 43,200 kg would enter from watershed runoff, and 800 kg would arrive in rainfall. Thus, sockeye carcasses supplied more than half of the lake's nitrogen influx (also true for phosphorus); both nitrogen and phosphorus were important in stimulating the lake's primary production. Notably, a deep long-term decline in marine-derived nitrogen and sockeye escapements occurred soon after commercial fishing began in 1882, as the fishery continuously removed salmon-carcass nutrients that otherwise would have entered Karluk Lake and supported its fertility. This historic decline was of longer duration and larger magnitude than any other variation of the 500-year record.

[68] See footnote 58.

The sediment cores were further examined for diatom algae and cladoceran zooplankton microfossils to understand the linkages between sockeye abundance, salmon-derived nutrients, and the primary and secondary productivity of Karluk Lake over the past 300–500 years (Finney et al., 2000; Sweetman and Finney, 2003). Most dramatically, the abundance and types of microfossils varied with past salmon escapements, decreasing or increasing as the lake's fertility shifted between oligotrophic, mesotrophic, and eutrophic states. In particular, the planktonic diatom *Stephanodiscus minutulus/parvus,* a species known to prefer mesotrophic to eutrophic conditions, varied directly with salmon escapements over the past 300 years. In contrast, *Cyclotella comensis* and *Fragilaria brevistriata* var. *inflata,* both known to prefer oligotrophic or slightly meso-eutrophic conditions, and many benthic diatoms varied inversely with salmon escapements.

For zooplankton microfossils in the sediment cores, the abundance and size of the cladoceran *Bosmina longirostris,* a selective prey item of juvenile sockeye (Table 4-14), varied directly with salmon escapements. This response indicated that *Bosmina* was controlled by salmon-derived nutrient loading, not by fish predation, a surprising result considering that large numbers of planktivorous sockeye young and sticklebacks resided in the lake. Likewise, indirect evidence suggested that the copepod *Cyclops,* the most abundant macrozooplankter in Karluk Lake, also varied directly with salmon escapements.[69] Thus, tight linkages existed between the sockeye escapements, salmon-derived nutrients, and Karluk Lake's primary and secondary production over the past 300–500 years. These results suggested that a positive feedback mechanism operated for Karluk's sockeye salmon over a fairly wide range of escapements—returning adults added carcass nutrients to the lake, nutrients enhanced the lake's primary productivity, the zooplankton food base increased, the growth of young sockeye improved, abundant high quality smolts migrated from the lake, and future adult runs increased.

The sediment record for Karluk Lake was not unique for southwestern Alaska; cores taken from the bottom of other sockeye salmon nursery lakes on Kodiak Island (Red Lake and Akalura Lake) and at Bristol Bay (Ugashik Lake and Becharof Lake) had similar profiles of marine-derived nitrogen (or escapements) to that in Karluk Lake. The sediments of all five lakes recorded low sockeye abundances in the early 1700s, early 1800s, and mid to late 1900s. In contrast, two control lakes (Frazer Lake and Tazimina Lake), both devoid of sockeye salmon for most of their existence, lacked the distinctive nitrogen isotope profile of the other lakes.

The region-wide similarity of escapement in the five nursery lakes over the past 300 years strongly suggested that large-scale factors, such as ocean climate and commercial fishing, had controlled the abundance of sockeye salmon. During most pre-fishery years, the sockeye escapements and ocean surface temperatures in the Gulf of Alaska varied similarly. For example, the pronounced low returns of sockeye in the early 1800s coincided with low ocean temperatures. Yet, a close link between sockeye abundance and ocean surface temperatures was not apparent during the commercial fishing years at Karluk because the harvests removed the salmon-carcass nutrients destined for the lake and disrupted the positive feedback mechanism. Based purely on the ocean climate, most of the commercial fishing era should have experienced stable or increasing sockeye escapements, not the long-term decline that actually occurred. The high rates of smolt-to-adult survival recorded in the 1900s also indicated that this was a particularly favorable period in the ocean environment, but lake fertility did not benefit then because substantial quantities of the salmon-carcass nutrients never reached the lake. Thus, both ocean climate and commercial fishing influenced the quantity of salmon-derived nutrients that entered Karluk Lake and altered its productivity.

Continuing with the paleolimnological studies of Karluk Lake, longer sediment cores (about 1.1 m) were collected in 1996 to reconstruct the changes in sockeye abundance over the past 2,200 years (Finney et al., 2002; Gregory–Eaves et al., 2003). These cores were analyzed for marine-derived nutrients (enriched in the stable isotope ^{15}N) and diatom microfossils to determine the long-term variations in sockeye abundance and lake fertility. These sediments revealed dramatic fluctuations of sockeye abundance over the past two millennia; the magnitude of the changes exceeded those of the historical record since 1882 and those of the past 500 years (Finney, 1998; Finney et al., 2000).

While many changes within the 2,200-year record lasted for only a few decades, most noteworthy were the long-term variations in salmon abundance that persisted for many centuries. For example, salmon were abundant (3,000,000 fish) in 200 BC, but then about 100 BC a long-term decline began that lasted for over 200 years and reduced sockeye numbers to very low levels

[69] Naiman et al. (2002) caution that the results for *Bosmina* may not apply to the entire zooplankton community, especially since copepods do not form fossils in the lake sediments.

(100,000 fish). These small runs were then followed by a mega-trend of increasing salmon abundance that continued nearly 1,000 years, from about 250 to 1,200 AD. Sockeye salmon were generally profuse at Karluk in 1,200–1,900 AD, followed by a substantial decline in the 1900s. Large fluctuations were not only evident in the salmon-derived nutrient data, but also in the abundance and types of diatom microfossils, as the lake shifted between oligotrophic and eutrophic states. Further, reconstruction of the past levels of total phosphorus in Karluk Lake showed that this lake nutrient tracked the nitrogen and diatom indicators.

The large and rapid decline in Karluk's sockeye abundance between 100 BC and 100 AD was likely caused by large-scale changes in the ocean's climate. The positive feedback mechanism still operated under these natural adverse conditions, though in an opposite direction—fewer adult salmon transported fewer carcass nutrients to the lake, reducing its fertility and ability to produce sockeye juveniles and future adults. This unfavorable ocean environment influenced salmon abundance on a regional basis, not just at Karluk. For example, a similar long-term signature occurred in the sediments of Akalura Lake, another sockeye nursery lake on SW Kodiak Island. However, in direct contrast to Karluk and Akalura lakes, Frazer Lake, which lacked sockeye salmon until 1951, had no long-term variation in its sediment profile over the past two millennia. Thus, the observed variations in salmon-derived nutrients could not be explained by local climatic factors at each lake. Instead, the long-term changes in sockeye abundance at Karluk appeared to be controlled by large-scale changes in ocean climate, along with salmon-derived nutrient loading of the lake and the positive feedback mechanism.

The long-term sediment record from Karluk Lake allowed biologists to understand for the first time the natural variability of sockeye salmon abundance before commercial fishing began in 1882. This was an important advancement because it had often been assumed that pre-fishery sockeye runs were always large, especially since the early fishery continued to reap huge harvests for a number of years (≥3,000,000 fish annually in 1888–94). The total sockeye run at Karluk in the early fishery, including the escapements, possibly reached 4,000,000–5,000,000 fish annually. The sediment record, however, showed that pre-fishery sockeye abundance was not fixed at a high level; instead, large natural variations had occurred centuries and millennia before any commercial fishing. In fact, the lowest sockeye abundance of the past 2,200 years (100,000 fish) occurred about 100 AD; these runs were even less than those reached during the historically low period of the 1950s–1980s. Despite the natural variations, commercial fishing profoundly diminished sockeye abundance at Karluk in 1890–1985, and the rapidity and magnitude of this decline was only previously matched by that of 100 BC–100 AD.

While the indigenous people of Karluk have harvested sockeye salmon from the river for many millennia, their total subsistence needs and fishing methods were such that they probably had little impact on overall fish abundance. The river barricades they built to help capture the salmon were opened once sufficient winter provisions had been secured (Moser, 1899). Yet they may have found it difficult to secure enough sockeye when the runs were sparse in the decades around 100 AD. In fact, some evidence suggests that natural fluctuations in sockeye abundance over the past 2,200 years did influence the timing of different cultural and archaeological phases of the Alutiiq people on Kodiak Island (Finney et al., 2002).

Although the controlling influence of ocean climate on fishery populations has been increasingly appreciated since at least the 1990s (Beamish and Bouillon, 1993; Martinson et al., 2008, 2009a, b), the paleolimnological studies of sediments at Karluk Lake were crucial for understanding the relative importance of natural factors and commercial fishing on sockeye salmon abundance. The sediment cores showed the overriding importance of ocean climate on natural cycles of abundance. These observed changes extended over decadal and multi-century timescales. Because of the confounding effects of commercial fishing, it had previously been difficult or impossible to recognize these broad natural changes when just the historical record from Karluk was examined, even though this record did show that commercial harvests significantly affected lake fertility and salmon abundance.

From a management viewpoint, the fact that sockeye salmon abundance at Karluk exhibit large and sustained natural variations that are primarily controlled by the ocean's climate is sobering. It would appear that management actions during neutral or favorable periods of ocean climate, and for brief adverse periods, can significantly affect the lake's fertility and sockeye abundance. But during adverse eras that last many decades or several centuries, to say nothing of a mega-trend lasting a millennium, there seems to be few management options that would sustain the system's high productivity. During long adverse periods, the benefits of lake fertilization to boost sockeye abundance may be entirely canceled during the ocean life phase, making it difficult to sustain an enrichment program for many decades.

The 2,200-year sediment record from Karluk Lake is exceptional in spanning a substantial part of the recent evolutionary history of sockeye salmon in this lake-river ecosystem, which last reopened access to anadromous fishes some 10,000 years ago when the glaciers retreated. The record demonstrates that Karluk's sockeye salmon possess the adaptations and genetic resources to withstand large environmental challenges and recover from extremely low levels that may last for centuries. This ability aptly demonstrates Thompson's insight (1950) that sockeye salmon possess considerable resiliency to environmental changes and fishing harvests. Notably, even the long-term decline that sockeye salmon experienced in the 1900s was within the evolutionary survivability of this species. The tenacity and resiliency of sockeye salmon engenders admiration for this resourceful and diverse species.

Though the 2,200-year paleolimnological record at Karluk has given many new insights into the population dynamics of sockeye salmon, this study anticipates even further discoveries from earlier lake sediments deposited shortly after the glaciers first retreated from SW Kodiak Island. Such early records may reveal 1) the level of sockeye abundance that was first maintained purely by natural nutrient inflows from the local watershed and atmosphere, and 2) the number of years that passed before sockeye-carcass nutrients significantly modified the fertility of Karluk Lake. Both results would give insights into natural ecosystem functioning.

While adult sockeye salmon transport large quantities of marine nutrients to Karluk Lake and affect its fertility, they also carry other chemical elements and compounds that may have detrimental effects on the ecosystem. For example, Krümmel et al. (2003) reported that the sockeye salmon of SW Alaska accumulated polychlorinated biphenyls (PCBs), a toxic pollutant, from the very low concentrations in the ocean and released them into their natal spawning lake. They estimated that 1,000,000 adult salmon would deliver more than 160 g of PCBs to the lake, though the impact of this chemical on the ecosystem was unknown.

Sockeye Salmon Abundance: Ocean Climate and Karluk Lake Fertility

Many theories have been advanced over the years to explain the variations in abundance of Karluk's sockeye salmon, especially its long-term decline. This has been a difficult task because there are many possible factors that affect abundance and the complex life cycle of sockeye salmon takes place in two aquatic environments—the smolt-to-adult marine phase and the egg-to-smolt freshwater phase. Once it had been determined during the 1920s–1940s that smolt-to-adult survival rates were exceptionally high for Karluk's sockeye, the marine phase of the life cycle seemed to be a rather benign environment for the salmon, and biologists then focused their attention on the possible controlling factors in freshwater. Yet, both marine and freshwater environments determine the success of this species. In this regard, studies of the limnology and paleolimnology of Karluk Lake have been crucial in understanding at least two natural controls of sockeye salmon abundance—the ocean climate in the marine life phase and lake fertility in the freshwater life phase.

The end products of the Karluk Lake ecosystem are its smolts, while the end products of the ocean environment are its adults. The numbers, size, and condition of sockeye smolts are a grand summation of an array of rearing factors in the lake, and the qualities distilled into these young fishes often determine their later success in the ocean and survival to adulthood. Apparently, the most important freshwater factor for smolt production, however, is lake fertility, the ability to produce the zooplankton foods that nourish young sockeye over several years. The abundance of returning sockeye adults is often strongly linked to the number and condition of smolts produced each year, but the ocean environment, especially large-scale climatic factors, can independently control the number of adults that return to Karluk Lake and influence its fertility. The size and condition of sockeye adults are determined by their ocean residence. Hence, ocean climate and lake fertility are fundamental controlling factors of sockeye salmon abundance at Karluk, with ocean climate being the ultimate long-term determinant.

Based on knowledge gained from limnological and paleolimnological studies of Karluk Lake, the interactions of the freshwater and marine life phases of sockeye salmon can be summarized in two simplified models: 1) the natural pre-fishery conditions that existed for many millennia, and 2) the century of intense fishery and declining sockeye runs that occurred in 1886–1985 (Fig. 7-10). Under natural pre-fishery conditions, sockeye adults that return to spawn in their natal waters at Karluk Lake not only transport their reproductive products upstream, but also bring substantial amounts of marine-derived nutrients to the lake. This nutrient influx supports the lake's fertility by enhancing phytoplankton production and the zooplankton food base of young sockeye. If the number of returning adults happens to increase for a number of years because of favor-

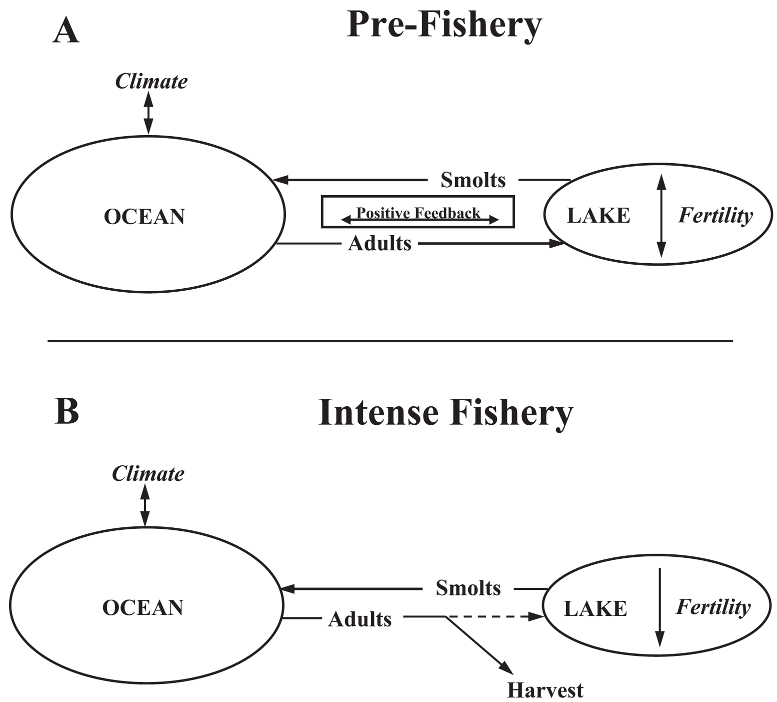


Figure 7-10. Simplified model of the interactions and main controlling mechanisms of Karluk's sockeye salmon under pre-fishery conditions (A) and intense fishery conditions (B).

able ocean conditions, the subsequently higher nutrient inflows raise the lake's fertility and produce more and better smolts. This enhancement leads to even higher adult returns.

Such a reinforcing cycle between ocean climate, lake fertility, smolts, and adults is a positive feedback mechanism, a somewhat unusual and potentially unstable situation in nature if extended too far, since it either drives the population to low levels or increases it to unsustainable heights. For such a feedback loop, the future abundance of adult sockeye is partially a function of its present abundance. Of course, positive feedback can also work in the opposite direction when adult numbers decrease, reducing lake fertility, smolts, and future adult returns. Thus, positive feedback can act to either enhance or reduce sockeye abundance. For the Karluk ecosystem, positive feedback appears to operate over a fairly wide range of sockeye abundance, though other factors undoubtedly become more important at extremely low and high population levels. More typically in nature, a negative feedback system operates to control population numbers by opposing, not reinforcing, both positive and negative changes in abundance.

Under natural conditions, lake fertility and sockeye abundance at Karluk are ultimately determined by large-scale ocean phenomena, most likely by climatic factors. If the ocean climate remains stable or randomly fluctuates up and down every few years, not much change occurs in lake fertility and sockeye abundance. There may even be short periods when the effects of ocean and lake conditions counteract each other. For example, particularly favorable lake conditions in producing sockeye smolts can be temporarily overridden by adverse ocean climates. But if the ocean climate has long-term positive or negative variations, say of ten years or more, the positive feedback mechanism drives sockeye abundance to a new level as lake fertility adjusts to the new quantities of salmon-carcass nutrients. Thus, large and sustained changes in ocean climate produce large variations in sockeye abundance under natural pre-fishery conditions. The two environments and life phases are linked by the positive feedback mechanism.

Natural fluctuations in sockeye salmon abundance are buffered by a wide range of physical and biological factors in Karluk Lake and the ocean. First, Karluk Lake has an overall water-residence time of about 5 years; it varies from 1.3 years in the Thumb basin, to 3.7 years in the north basin, and 7.1 years in the south basin (Table 7-1). Consequently, it takes a number of years before the lake's water chemistry, nutrients, and fertility adjusts to new levels of salmon escapement. Koenings and Burkett (1987b) estimated that it would take 5–8 years to reach a new steady-state phosphorus level after a change in nutrient loading to Karluk Lake. Second, it takes a number of years for climatic changes to affect the large water masses of the North Pacific Ocean. Third, sockeye salmon have a complex, multi-year, life cycle and a wide diversity of adaptations, such as the

presence of many subpopulations, the many combinations of freshwater and ocean ages, and a wide range of seasonal run times and spawning sites. Fourth, the exchange of salmon-derived nutrients at Karluk Lake occurs between parent and offspring, subpopulations, year classes, and salmon species. All of these moderating influences and lag effects create an inertia that must be overcome, possibly lasting several years or a decade, before salmon-derived nutrient inputs and lake fertility are significantly altered at Karluk.

Once an intense commercial fishery on sockeye salmon began at Karluk in 1882, the positive feedback connection between the ocean and lake environments was disrupted (Fig. 7-10). Even if favorable marine conditions produced higher returns of adult sockeye, the fertility of Karluk Lake was not enhanced because salmon-carcass nutrients that would have entered the lake were now removed in the fishery. For example, during 1888–94 enormous runs of sockeye returned to Karluk and over 2,500,000 fish were harvested each year. The removal of these adults substantially reduced the inflow of salmon-carcass nutrients to the lake. Instead of benefiting Karluk Lake during a period of advantageous ocean conditions, lake fertility and smolt production began to decline, jeopardizing future run abundance. A more serious impact on sockeye abundance occurs when adverse marine conditions and intense fishing overlap. This detrimental combination rapidly decreases the inflow of salmon-carcass nutrients, reducing the lake's fertility and its ability to produce sockeye smolts. Of course, because of the natural inertia within the Karluk ecosystem, it took a decade or more before it became evident that the runs were declining in the early fishery. Thus, the huge loss of salmon-carcass nutrients in the fishery blocked the positive feedback mechanism between the ocean and lake environments.

The fertility of Karluk Lake is responsive to the changing inputs of salmon-carcass nutrients, more so than for many other Alaskan lakes. This was seen in Karluk Lake's diatom flora (>300 taxa), which is sensitive to nutrient levels (Gregory–Eaves et al., 2003). Most dramatically, Karluk and Fraser lakes have completely different arrays of diatom microfossils in their sediments, even though both lakes are physically similar and located in adjacent watersheds. Numerous sockeye salmon have returned to Karluk Lake for many millennia and continually added marine-derived nutrients that altered the lake's fertility and diatom flora. In contrast, an impassable waterfall prevented sockeye from reaching Fraser Lake for many thousand years and blocked the entry of salmon-carcass nutrients. Consequently, Fraser Lake developed a completely different diatom flora.

Compared with other sockeye salmon nursery lakes in southwestern Alaska, Karluk Lake is dependent on salmon-derived nutrients to sustain its productivity, though the reasons for this sensitivity are not entirely clear. Of primary importance is the fact that a significant portion of the annual influx of nitrogen and phosphorus, key nutrients that stimulate primary production, come from salmon carcasses (Koenings and Burkett, 1987b; Schmidt et al., 1998; Finney, 1998).[70] Typically, smaller amounts of these nutrients come from watershed inflows and direct rainfall. Watershed characteristics such as tributary area, topography, and geology undoubtedly restrain the amounts of inflowing nutrients from inorganic sources. Because the lake is surrounded by steep mountains, most inflowing streams have short lengths and their waters quickly reach the lake before remaining long in contact with soils and inorganic sediments to gain nutrients. Also, since the surface area of Karluk Lake makes up 14% of its total drainage basin (Fig. 1-5), a significant portion of its annual inflow of water comes directly to the lake's surface via rainfall, without any chance of getting additional nutrients by chemical dissolution or mechanical weathering processes of mineral and sedimentary sources. In particular, this direct rainfall route would reduce phosphorus inputs by bypassing the traditional geologic source of this nutrient. The non-carcass nutrient sources are, nevertheless, important in setting a lower limit to the fertility of Karluk Lake (and the positive feedback mechanism) that is independent of sockeye escapement.

In comparing sockeye salmon nursery lakes in Alaska, it is unclear if the positive feedback mechanism described for Karluk Lake is unique to that lake or more widespread. The nutrient sensitivity of Karluk Lake is one reason why positive feedback operates so strongly there. But the Karluk ecosystem possesses other characteristics that appear to support the positive feedback mechanism. A particularly important feature of the Karluk system is that its total spawning area for sockeye salmon is limited and cannot greatly expand in years when escapements are large. For example, in 1926 when over 2,500,000 sockeye reached the spawning grounds from a total run of over 4,500,000, many females died before spawning.[71] Escapements of this magnitude go

[70] See footnote 35 (2).

[71] The dry conditions in 1926 that caused low water levels and

Pair of spawning sockeye salmon, Karluk Lake tributary, ca. 1932. (Joseph Thomas Barnaby, from Lynn L. Gabriel, Herndon, VA)

well beyond those needed to fully seed all available spawning areas. Burgner et al. (1969) estimated that the Karluk system had 349,100 m² of sockeye spawning area, apportioned by lake beaches (12,500 m²), lateral streams (16,700 m²), terminal streams (67,100 m²), and the upper 5 km of the Karluk River (252,800 m²). Based on an estimated average redd size of 2 m² and two adults per redd, potentially an escapement of 349,100 could fully seed the spawning area if they were 100% efficient.

Because of spawning inefficiencies, repeated spawning of the same area by spring and fall runs, bear predation and other losses, and incomplete data on the areas of lake beach used, the Karluk system needs more spawners than the minimum calculated above for full seeding, the number possibly approaching 1,000,000 fish. When ADFG biologists surveyed the spawning areas at Karluk in 1973, they estimated that it contained 802,000 m², the majority being the 468,499 m² found along the lake's beaches.[72] Their estimate indicated that full seeding of the available spawning area would require more than 800,000 fish. We do not know which spawning area estimate is correct, but both escapement levels were easily reached during the early fishery years and into the 1930s. Yet, during the 1950s–1980s, escapements declined to such low levels that the potential spawning area must have been under-seeded.

Spawning limitations in the Karluk system mean that extremely large escapements cannot swamp the lake-rearing habitat with myriad young sockeye that deplete their zooplankton foods. Instead, the lower abundance of young sockeye exert less predation pressure on zooplankton populations, which then are mostly controlled by phytoplankton production and ultimately by lake fertility. Adults that fail to spawn in years of large escapements are not wasted in the system, but benefit the rearing juvenile sockeye by adding salmon-carcass nutrients to the lake. That is, large escapements beyond that needed for adequate spawning contribute to the lake's fertility and success of young sockeye. In contrast, if excess adults of large escapements successfully spawned and produced millions of additional fry to rear in Karluk Lake, the zooplankton food base would be depleted and the growth and success of young sockeye reduced. This situation describes the traditional density-dependent condition, or negative feedback mechanism, that exists for sockeye salmon in many other Alaskan lakes. For a positive feedback mechanism to operate, it would appear to be a necessary condition that juvenile sockeye do not deplete the lake's zooplankton to such an extent that intra-specific competition becomes intense. This aspect of the breeding and rearing system of Karluk shifts this lake ecosystem to one that is influenced by lake fertility and dependent on salmon-carcass nutrients.

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higher water temperatures at Karluk Lake also may have hindered the spawning of sockeye salmon.

[72] The spawning areas at Karluk were apportioned by the ADFG in 1973 into Karluk Lake beaches (468,499 m²), upper Karluk River (111,693 m²), O'Malley Lake shore (108,402 m²), Thumb Lake tributaries (40,164 m²), Karluk Lake lateral tributaries (28,782 m²), Karluk Lake terminal tributaries (19,904 m²), O'Malley River (8,953 m²), Lower Thumb River (8,830 m²), Thumb Lake shore (6,169 m²), and O'Malley Lake tributaries (500 m²). White, Lorne E. 1976. Karluk sockeye restoration. Project Brief. ADFG, FRED (December, 1976). Unpubl. report. 68 p. Located at ADFG Office Files, Kodiak, AK.

Spawning sockeye salmon and carcasses, Karluk Lake tributary, ca. 1932. (Joseph Thomas Barnaby, from Lynn L. Gabriel, Herndon, VA)

When biologists first explored the sockeye salmon breeding grounds at Karluk Lake in the early 1900s, many were surprised that the spawning areas and substrates seemed to be insufficient to support the huge runs that returned each year. Instead of finding large deep tributaries with ample areas of properly sized gravel, many lateral tributaries seemed too small, steep, and shallow, and their cobble substrates seemed too large for good spawning. Many streams had impassible barriers that restricted spawning to the lower reaches, while other streams were too shallow to cover the backs of spawning sockeye. Some lateral streams had flows too low for summer spawning, and were only useable by spring-run sockeye. Likewise, much of the lake's shoreline was composed of large cobbles unsuitable for spawning, though appropriate gravels did occur near the mouths of the Thumb and O'Malley rivers and at some other inflowing creeks. The few terminal streams that entered the lake appeared to be better spawning habitats, with improved flows and substrates, and the upper Karluk River provided a large spawning area for fall-run sockeye. Chamberlain (1907) declared that "Karluk Lake has many tributary creeks that are used by spawning fish, but the total area seems scarcely commensurate with the enormous productiveness." He further reported that many tributaries had cobble substrates too large for sockeye to move, and this caused spawned eggs to remain unburied and be washed downstream. When Karluk Lake was visited by APA hatchery superintendent Ingwald Loe in 1910 and by USBF inspector Ward Bower in 1911, they both felt that most sockeye spawning occurred in the shallow waters along the lake's shoreline and that the tributaries were too small and had unsuitable substrates. Gilbert and O'Malley (1920) concluded in 1919 that the natural spawning habitats at Karluk were poor and felt that a hatchery at the lake would benefit sockeye production:

> [Karluk Lake, 25–26 July 1919] These streams seemed wholly unfitted for spawning. They were short, violently rapid wherever seen, and appeared to be without quiet gravelly reaches where spawning could be successfully accomplished. The shallower portions of the lake, in depths where fish frequently spawn, were on the west side also for the most part totally unsuited for spawning. The bottom was thickly covered with coarse cobblestones and bowlders, without finer materials in which nests could be excavated . . . No gravel bars or quiet reaches were seen, and while these streams were the least unfavorable of those observed entering the lower half of the lake, it seemed incredible that any large number of salmon could successfully conceal their eggs in the narrow sand intervals between the rocks . . . The writers were impressed with the unfavorable nature of the grounds examined, by their small extent, and by the unbroken succession of spawning fish which continue to occupy these small creeks during the long season. Enormous waste of eggs must accompany this condition . . . it is believed that a red-salmon hatchery on Karluk Lake would operate to the very material advantage of the salmon run.

Shuman found considerable spawning activity along the lake's beaches in July 1943, but he decided that the short inflowing creeks were less important sites. He declared that "the amount of spawning gravels hardly seems to account for the great productivity of this system. Certainly some spawning areas—other than those of the few short streams—must play an important role in the productivity."[73] In the 1960s when

[73] Shuman, Richard F. 1943 notebook (16 July). Located at NARA, Anchorage, AK.

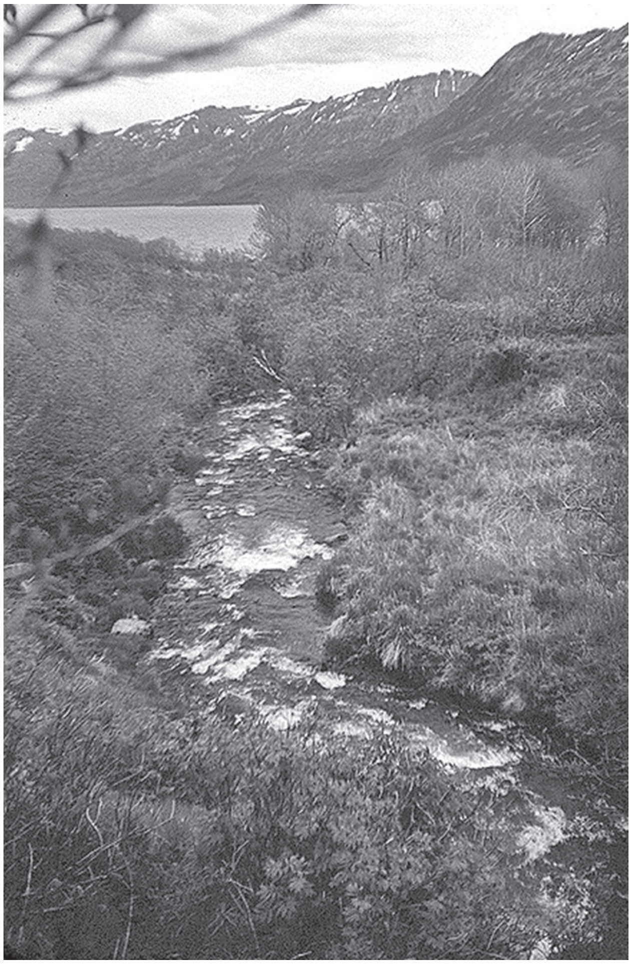
biologists compared the spawning areas and substrates in the Karluk and Brooks river systems, they found dramatic differences and were mystified how Karluk produced such abundant sockeye runs since the spawning conditions appeared to be adverse.

David Hoopes (1962) examined the physical properties of several tributaries to Karluk Lake and found that 90% of the sockeye spawned within the first 610 m. These small creeks were typically less than 3 m wide and seldom had a depth of more than 20–30 cm. They usually lacked refuge pools for the salmon, but instead were a succession of shallow riffles and scattered large rocks that became more abundant upstream. The coarse substrates in these streams restricted the spawning to small scattered pockets of gravel, but even there many loose eggs were evident and attested to the difficult conditions. Hoopes concluded that "In spite of the seemingly adverse spawning conditions present, each of the major lateral streams in the Karluk system annually support individual runs of sockeye salmon larger than the highest run recorded for Hidden Creek [at Brooks Lake] during this study. Whatever the factors may be that enable these streams [at Karluk] to support spawning runs of such magnitude, the fact remains that the races entering these streams to spawn are adapted to a set of environmental conditions markedly unlike those encountered in the lateral spawning tributaries of Brooks Lake." In fact, the large rocks in Karluk's tributary creeks allowed for higher spawning densities by physically delimiting smaller redd areas defended by sockeye (Hartman et al. 1964). For example, redd territories were less than 1 m^2 in some Karluk creeks, but exceeded 4 m^2 in the Brooks River. Thus, the limited and coarse spawning areas at Karluk were partially offset by increased redd densities and, in some habitats, by spreading out the spawning effort across spring and fall seasons.

Contrary to the conditions found in many other Alaskan lakes, there is little evidence that the growth of young sockeye in Karluk Lake, as influenced by the zooplankton forage base, is strongly density dependent. Burgner (1991) stated that "there is no evidence of density-dependent growth of sockeye" in Karluk Lake, while Koenings and Burkett (1987b) concluded that "the density of sockeye fry was well below lake carrying capacity." Likewise, Nelson et al. (2005) found for Karluk Lake that "under current conditions and escapement levels, the rearing environment is not limiting production." Schmidt et al. (1997) argued that as lake fertility declines, the forage base also declines and the system becomes more density dependent. Conversely, as salmon-carcass nutrients enrich a lake, it becomes less density dependent and this reduces the controlling effects of fish predation on the zooplankton.

Schmidt et al. (1998) showed that both lake fertility and fish predation influenced the zooplankton of Karluk Lake during 1980–94. Although it was not entirely clear which factor dominated in their study, lake fertility seemed to govern this interaction over the long-term, while fish predation had less influence. However, their 1980–94 study period followed 25–30 years of low escapements and nutrient inflows to Karluk Lake (Fig. 1-3), and fertility then must have been much lower than normal. If ever there was a time when Karluk Lake's fertility was greatly depleted and the potential for density dependent growth was high, it was in those years just before and after 1985. Additionally, it appears that an in-

Sockeye salmon spawning habitat in Grassy Point Creek, a lateral tribuary of Karluk Lake, August, 1958. (Auke Bay Laboratory, Auke Bay, AK)



Meadow Creek, a sockeye salmon spawning tributary at the south end of Karluk Lake (in distance), ca. 1952. (Charles E. Walker, Sechelt, BC)

verse relationship between zooplankton grazer biomass and sockeye escapement (used as a proxy for fry abundance) would be expected during 1980–94 for spawning reasons alone. During this 15-year period, escapements varied over a wide range, from about 150,000 (under-seeded) to 1,100,000 (fully-seeded), but for most years the spawning grounds were under-seeded. When under-seeded, sockeye fry abundance and predation on zooplankton should vary directly with escapement size. But if the number of spawners consistently exceeded the fully-seeded limit, fry abundance would be bound by the physical limit on spawning, not by escapement numbers. In that case, zooplankton grazer biomass may vary directly with high escapements as the lake's fertility benefited.

Perhaps the strongest evidence that Karluk Lake's fertility exerts more control on zooplankton abundance than does fish predation was shown by the 500-year microfossil record in the bottom sediments (Sweetman and Finney, 2003). The abundance and body size of the cladoceran zooplankter *Bosmina*, a preferred food of young sockeye, varied directly with sockeye escapements and salmon-carcass nutrients over the past 500 years. If young sockeye had intensely competed for *Bosmina*, the abundance and body size of this prey item should have varied inversely with escapement. When the fertility of Karluk Lake declined during the 1900s, *Bosmina* abundance and body size also declined, indicating that the rearing environment shifted at least somewhat toward greater density dependence. Sweetman and Finney (2003) concluded that in Karluk Lake, "salmon-derived nutrients ultimately controlled the response of zooplankton, and predation by juvenile sockeye salmon appears to have little impact on trophic dynamics."

Sockeye salmon spawning habitat in Moraine Creek, a lateral tributary of Karluk Lake, September 1959. (Auke Bay Laboratory, Auke Bay, AK)

The influx of salmon-carcass nutrients to Karluk Lake varies bimodally during the run season. Spring-run sockeye, which spawn in the lateral and terminal tributaries of the lake, contribute all of their carcass nutrients to Karluk Lake and add to its fertility. Yet only those fall-run sockeye that spawn in terminal streams and lake beaches add nutrients to the lake. In contrast, the nutrients of fall-run sockeye that spawn in the upper 5 km of the Karluk River wash downstream and never add to the lake's fertility. These carcass nutrients enhance the river's productivity and may partially benefit offspring that spend their first few months feeding in the river before migrating to the lake. But river offspring eventually move upstream to their long-term rearing environment in the lake and benefit from the nutrient and fertility enhancements provided by other sockeye subpopulations. These different fates of the salmon-carcass nutrients highlight an important reason why sockeye salmon, throughout their North American and Asian range, typically spawn in lake tributaries and beaches—their nutrients flow to the nursery lake and eventually benefit their offspring. From an evolutionary viewpoint, it is difficult to imagine that sockeye salmon would vigorously persist if they only spawned in the river below a lake and their offspring forwent the carcass nutrient benefits.

Of all the species of Pacific salmon in Alaska, sockeye salmon appear to be the most likely to have a positive feedback mechanism between adults and smolts. Chinook, coho, and chum salmon and steelhead are not so abundant in the Karluk system that they significantly influence the lake's fertility. Furthermore, the offspring of these species do not depend on the lake rearing habitat and zooplankton food base for survival. Besides sockeye salmon, only pink salmon return to Karluk in large enough numbers to potentially add significant amounts of salmon-carcass nutrients to the lake. Yet pink salmon only rarely reach Karluk Lake in large numbers; these fish more typically spawn in the Karluk River. Even if significant numbers of pink salmon adults did reach Karluk Lake, their offspring reap few benefits of the enhanced fertility since young pink fry return to the ocean soon after emerging from the substrate. Schmidt et al. (1998) concluded that pink salmon had little net impact on the sockeye salmon of Karluk.

After more than 100 years of fisheries research at Karluk, it is well-appreciated that sockeye salmon are exquisitely adapted to this pristine ecosystem and their success is closely linked to conditions in the lake. Further, it is clear that sockeye salmon not only respond to the lacustrine environment, but, in fact, modify their own rearing habitat and future production. Species with such direct impacts on the structure and function of an ecosystem are often recognized as keystone species; this designation certainly applies to the sockeye salmon of Karluk. By annually transporting substantial quantities of marine nutrients to Karluk Lake, they immediately influence the lake's fertility and plankton communities. Furthermore, the effects of their physical body mass and nutrients ramify throughout the ecosystem, with significant impacts on other resident fishes (stickleback, charr, sculpin, coho salmon), mammals (brown bear, red fox, river otter), birds (bald eagle, merganser, sea gull, tern), benthic invertebrates, and various internal and external parasites, to name just a few obvious components. Many of these interrelationships, while still not well known, are nevertheless evident to field biologists who have witnessed the seasonal movements, behaviors, and concentrations of the region's fauna.

Summary and Conclusions

Limnological and paleolimnological research at Karluk Lake has had a remarkable history since 1926. This work led to the current understanding of linkages between ocean environment, lake fertility, and sockeye salmon productivity. During the first 25 years of the fishery, the lake ecosystem was thought to be relatively unimportant to sockeye salmon, but that view changed around 1905–10 with the discovery that juveniles reared in these freshwaters for a year or more and fed on its plankton. The planktonic foods of juvenile sockeye appeared to be linked to the amounts and timing of nutrient inflows to the lake. This caused Willis Rich to speculate in 1926 that the growth and survival of juvenile sockeye were linked to nutrients leached from adult salmon carcasses. Biologists irregularly studied the lake fertility idea in the 1920s–1940s; this eventually led to the fertilization experiment at Bare Lake in the 1950s. Lake fertility was investigated again with renewed vigor using modern equipment and methods in the 1980s–1990s, including stable isotopes to study food webs, past productivities, and linkages between adult escapements and lake nutrients. This research clearly demonstrated the importance of salmon-carcass nutrients to sockeye salmon production at Karluk Lake. It also showed that the ultimate natural control of lake fertility and sockeye abundance is the ocean climate, which can produce profound long-term fluctuations in sockeye salmon numbers.

Historical studies of Karluk Lake's limnology were connected with knowledge about the life cycle of sockeye salmon. Compared with all other species of Pacific salmon, sockeye possess unique features in their life history, behavior, and morphology. During their annual spawning migration to freshwater, sockeye nearly always ascend river systems that have a lake, which functions as a juvenile rearing habitat for one or more years. Since adults typically spawn in lake tributaries or shoreline habitats, most salmon-carcass nutrients return to the lake and benefit their offspring.

Sockeye juveniles and adults are morphologically and behaviorally adapted to feed on planktonic animals. Juvenile sockeye feed on the lake's macrozooplankton, which in turn consumes, or indirectly relies on, the abundant phytoplankton crop. Phytoplankton production in Karluk Lake depends on the annual release of nitrogen and phosphorus nutrients from the decomposing carcasses of post-spawning adult salmon. Because salmon-carcass nutrients benefit the planktonic food chain that supports young sockeye, the lake produces numerous large smolts that return as adults after several years in the ocean. Sockeye salmon success in the ocean is governed by large-scale climatic conditions. A direct nutrient link exists between parents and offspring and between the marine and freshwater environments.

Under natural conditions, a positive feedback mechanism exists between the adults and juveniles of Karluk's sockeye salmon. This interaction exists over a rather broad range of escapements. During benign ocean climates, large returns of adult sockeye salmon transport large amounts of nutrients to Karluk Lake that enhance its fertility and the food chain that supports juvenile sockeye. This leads to higher smolt production and abundant future runs of adults. That is, success of juvenile sockeye salmon is directly related to adult escapement size, while escapement size is at least partially related to juvenile success. Large-scale ocean phenomena have an independent control on escapement size. Of course, the positive feedback mechanism would not continue to operate indefinitely, and salmon abundance would eventually be controlled by other physical or biological factors. During an intense fishery on sockeye salmon, annual harvests remove nutrients that were destined to sustain plankton production and juvenile growth in Karluk Lake. The long-term decline of sockeye salmon at Karluk between 1890 and 1985 appears to have been caused by the continual loss of salmon-carcass nutrients to the lake, reducing its fertility and ability to produce smolts. This long-term downward trend was reversed after 1985 by increasing escapements and salmon-carcass nutrients to Karluk Lake.

CHAPTER 8

Stickleback—Juvenile Sockeye Salmon Interactions

Abundant sticklebacks—competitor, predator, or protector?

Threespine sticklebacks, *Gasterosteus aculeatus,* are common in Karluk's river-lake ecosystem. They occur in the littoral and limnetic waters of Karluk, Thumb, and O'Malley lakes, in slow currents along the Karluk River, and in the estuary at Karluk Lagoon. Almost every biologist who visited Karluk Lake since 1889 has commented upon the large abundance of sticklebacks and wondered how these small fishes affected its sockeye salmon. Opinions have varied widely about the impacts on sockeye, from being very harmful to somewhat beneficial. Thus, questions about the stickleback-sockeye interaction have persisted throughout Karluk's fisheries history. For instance, do sticklebacks compete with juvenile sockeye for the planktonic foods in Karluk Lake and thereby reduce sockeye growth and production? Since sticklebacks and juvenile sockeye are similarly sized, may use similar foods, and share rearing habitat in Karluk Lake, they would appear to vie for resources. Yet some biologists believe young sockeye are superior competitors to sticklebacks.

Further, as sockeye abundance declined at Karluk between 1890 and 1985, did stickleback numbers increase in Karluk Lake, filling the niche once occupied by juvenile sockeye and confounding efforts to restore the runs? Or, did stickleback populations concurrently decline with sockeye numbers because of reduced lake fertility? Conversely, do abundant stickleback populations relieve young sockeye from intense predation by larger fish? And, do sticklebacks prey on sockeye eggs, or do juvenile sockeye prey on sticklebacks? Overall, are Karluk's sticklebacks detrimental, beneficial, or of no consequence to juvenile sockeye salmon?

In this chapter we examine these persistent questions about threespine sticklebacks and juvenile sockeye salmon at Karluk. We recap studies of stickleback life history at Karluk Lake, summarize field observations of stickleback abundance, and discuss recent efforts to understand the stickleback-sockeye interaction. In the following discussion, we use the general term "stickleback" in reference to *G. aculeatus,* not to the ninespine stickleback, *Pungitius pungitius,* that has also been reported from Karluk Lake, though apparently it is rare (Greenbank and Nelson, 1959).

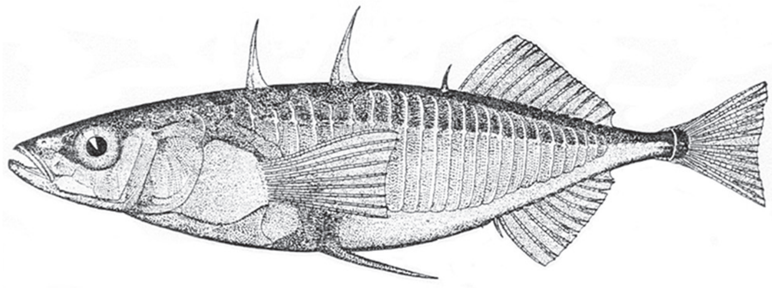
Stickleback Life History

Many life-history aspects of sticklebacks in Karluk Lake are fairly well known because of studies by Greenbank and Nelson (1959). They found that sticklebacks were evenly distributed in the shallow waters of Karluk Lake, except in May–June when dense schools migrated up the Thumb and O'Malley rivers to spawn in the two shallow tributary lakes.[1] Seasonal movements occurred within and between local habitats, but sticklebacks did not make far-ranging migrations to and from the ocean. Sticklebacks also inhabited the open surface waters of Karluk Lake. The only aquatic habitats lacking sticklebacks in Karluk's watershed were those lying above the impassable falls of tributary streams.

Greenbank and Nelson claimed that sticklebacks lived about 2¼ years and spawned at age-1 or -2 years, though more recent studies showed that most fish spawned at age-3 years and some reached 4 years.[2] Spawning occurred in June–July (and possibly August) in the aquatic plant beds at Thumb and O'Malley lakes and at a few littoral areas of Karluk Lake. Adults usually died after spawning.

[1] FWS biologist Philip R. Nelson apparently first noticed the mass migration of sticklebacks in the Lower Thumb River on 7 June 1955, but thought these fish were moving out of Thumb Lake. FRI biologist Charles E. Walker notified Nelson that the stickleback migration occurred there annually. Philip R. Nelson 1955 notebook (7 June) located at NARA, Anchorage, AK.

[2] Olson, Robert A., and Richard L. Wilmot. 1989. Karluk Lake sockeye salmon and threespine stickleback studies (1982 to 1988). USFWS, Region 8, Alaska Fish and Wildlife Research Center, Anchorage (29 June 1989). Unpubl. report. 56 p. Copy from Richard L. Wilmot, ABL, Auke Bay, AK.



Threespine stickleback. (Drawing by Albertus H. Baldwin, from Evermann and Goldsborough, 1907.)

Sticklebacks are sexually hermaphroditic, mature individuals having both ovaries and testes. A mature stickleback female was collected with eyed eggs in her ovaries, this possibly indicating self-fertilization. FWS biologist Charles Huver studied the stickleback's embryology at Bare Lake in 1955.[3] Eggs hatched in 9–14 days and growth lasted about four months (June–September) each year. The largest individuals in the lake reached 80 mm standard length at maturity, though Walker reported larger sticklebacks in Karluk Lagoon.[4] Rutter (1899) recognized two morphological forms of Karluk's sticklebacks: those with few lateral plates along their body and inhabiting lake and river freshwaters, and those with many lateral plates and inhabiting the saltier waters of Karluk Lagoon.

Sticklebacks mainly fed on small insect larvae and planktonic crustaceans, but did not consume sockeye eggs or fry, the eggs being too large for them to engulf whole. Direct Scuba observations of beach spawning sockeye recorded no egg predation by the abundant sticklebacks.[5] Stickleback and juvenile sockeye diets appeared to be similar, though comparisons were difficult since detailed food studies were lacking. Juvenile sockeye occasionally preyed on small sticklebacks. Arctic charr fed on sticklebacks and their eggs in Karluk Lake in June–July; Dolly Varden fed little on them. Greenbank and Nelson (1959) suggested that stickleback populations may benefit young sockeye by relieving them from Arctic charr predation. Other stickleback predators were sculpins (Greenbank 1966) and possibly rainbow trout and juvenile coho salmon. Sticklebacks served as hosts for several internal and external parasites; some of these parasites were transmitted to fish-eating birds, mammals, and other fishes when they ate infected sticklebacks.

Many fish-eating birds preyed on Karluk's sticklebacks, including gulls; kittiwakes; terns; mergansers; ducks; loons, *Gavia* sp.; kingfishers, *Ceryle* sp.; eagles, and magpies, *Pica* sp. Rutter saw magpies opportunistically feed on sticklebacks migrating up the Thumb River in 1903.[6] Rich concluded that gulls and terns commonly fed on sticklebacks at Karluk Lake, based on the fish remains he found around the nests on Gull Island in 1926. Morton (1942, 1982) examined the stomach contents of 25 fish-eating birds at Karluk Lake during 1939–41, primarily red-breasted mergansers and possibly kingfishers, terns, kittiwakes, and loons, and found that sticklebacks were the most common food. He claimed that sticklebacks sounded whenever terns flew overhead.[7] DeLacy checked the stomachs of 20 mergansers and one kittiwake at Karluk Lake and River in 1942 and found sticklebacks to be the most frequent prey; one individual had 12 sticklebacks.[8] Walker inspected the stomachs of fish-eating birds at Karluk Lake in 1953 and again found sticklebacks to be the most common food:

> [Karluk Lake, 1953] Birds in the area which prey on fish are the short-billed gull, glaucous-winged gull, Bonaparte gull, Arctic tern, merganser, and golden eye. The population size of Bonaparte gulls and Arctic terns is very small; it fluctuates from four to a dozen birds. The salmonids taken by those birds are probably coho which are in the surface waters at all times of the summer. The other birds are comparatively numerous but, with the exception of one red fingerling found in a mer-

[3] Huver studied (and sketched) the developmental stages of threespine sticklebacks. Charles W. Huver, Forest Lake, MN. Personal commun. with Richard L. Bottorff, 1997.

[4] Memo (20 August 1956) from Philip R. Nelson, Fishery Research Biologist, FWS, Seattle, WA, to John Greenbank, FWS, Juneau, AK. Located at NARA, Anchorage, AK.

[5] BCF. 1958–1960. Monthly research report. U.S. Department of the Interior, FWS, BCF, Alaska Region. Unpubl. report. (August 1959). ABL Office Files, Auke Bay, AK.

[6] Rutter, Cloudsley Louis. 1903. Notes made by Mr. Cloudsley Rutter at Karluk, season of 1903. Unpubl. notes. 7 p. Copy provided by Mark R. Jennings (Davis, CA) and located in Box 130, Barton Warren Evermann papers, Library Special Collections, California Academy of Sciences, San Francisco, CA.

[7] Morton, William M. 1941 notebook (9 August). Located in the personal papers of Robert S. Morton, Portland, OR.

[8] DeLacy, Allan C. 1942. Merganser food study, Karluk, 1942. Unpubl. data. 1 p. Located at NARA, Anchorage, AK.

Black-billed magpies, Karluk Lake, 1969. (Benson Drucker, Reston, VA)

Mew gull, Karluk Lake, 1969. (Benson Drucker, Reston, VA)

> ganser, stomach analyses revealed that stickleback was the fish eaten.[9]

Frank Carlson looked in the stomach of a mew gull, *Larus canus,* at Meadow Creek in 1956 and found several sticklebacks and an 80 mm coho fry.[10] Greenbank and Nelson (1959) stated that mergansers, gulls, loons, and kittiwakes preyed on sticklebacks. Gard examined 18 merganser stomachs at Karluk Lake in 1965 and found 39% with sticklebacks.[11]

Several mammals preyed on sticklebacks, including the brown bear and red fox. Walker observed red foxes searching the shorelines for sticklebacks as they migrated up Thumb and O'Malley rivers,[12] and Drucker photographed this hunting behavior in the 1960s. Mary Faustini, FWS biologist, again observed red foxes hunting sticklebacks along the O'Malley River in 1997.[13] Brown bears opportunistically fed on large stickleback accumulations in the O'Malley River.[14] Shorttail weasels, *Mustela erminea,* fed to a limited extent on small fish taken along lake and river shorelines (Feuer, 1958), and undoubtedly the river otter consumed sticklebacks in Karluk Lake and River.

Early Observations of Sticklebacks

Tarleton Bean (1891) first reported on the sticklebacks of Karluk Lake, claiming they were numerous in the lake's littoral and tributaries in August 1889. He feared that sticklebacks ate sockeye eggs. His observations indicate that sticklebacks have been abundant in Karluk Lake since the very beginning of its fisheries history, though actual population sizes remain unknown.

Rutter (1899) collected sticklebacks from Karluk Lake and Lagoon in 1896–97, but said nothing about their abundance. They must have been plentiful at the lake in 1903 since he incidentally caught many sticklebacks while sampling for young sockeye; a fyke net placed overnight at the lake's outlet on 25 June captured 530 sticklebacks (Chamberlain, 1907). Rutter was the first biologist to describe the mass spawning migration of sticklebacks up the Thumb and O'Malley rivers, a dramatic part of their life cycle:

> [Karluk Lake, 1903] Sticklebacks are exceedingly abundant in Karluk Lake and the marshes adjacent to the river. On June 1 we saw an immense school of this species in the stream connecting the main and side lakes. At that time the water was high and the rapids very strong. The sticklebacks were trying to go up stream, and the strong current had carried them over against one shore. They were able to stem the current up to a small rock that jutted out from shore, but they

[9] Walker, Charles E. 1954. Karluk young fish study, 1950–1954. Kodiak Island Research, FRI, University of Washington, Seattle, Unpubl. rep. Located at FRI Archives, University of Washington, Seattle.

[10] Carlson, Frank T. 1956 notebook (3 July). Located at NARA, Anchorage, AK.

[11] Gard, Richard. 1965. Merganser food habits study, 1965. Unpubl. data. 1 p. Located at NARA, Anchorage, AK.

[12] See footnote 9.

[13] Mary Faustini, FWS, Kenai, AK, personal commun. with Richard L. Bottorff, 1998.

[14] In the 1980s masses of sticklebacks accumulated below a temporary low-head dam placed in the O'Malley River by FWS biologists and brown bears used this opportunity to feed on these fish masses. Richard L. Wilmot, Auke Bay, AK, personal commun. with Richard L. Bottorff, 1996.

Red fox hunting sticklebacks, Karluk, 1960s. (Benson Drucker, Reston, VA)

could not pass that point, except that occasionally one would jump out on the bank and accidentally get back into the water on the upper side of the rock. Below the rock they were crowded into a mass so thick that several could be caught by making a grab with one hand. Magpies stood on the bank and picked them up at leisure. The school was from one to three feet wide, about a foot deep, and extended back along the shore for about 200 yards. The same point was visited July 1, and about the same number of sticklebacks was still there. The water had gone down the first of August and the school was not to be seen.[15]

This annual mass migration, a vivid demonstration of stickleback abundance, has been noted by biologists throughout Karluk's fisheries history.[16]

Evermann and Goldsborough (1907) mentioned that sticklebacks collected at Karluk by Rutter were 50–100 mm long. Sticklebacks of 100 mm total length were equivalent to the largest specimens (80 mm standard length) reported by Greenbank and Nelson (1959).

1926–37: Stickleback Observations by Rich and Barnaby

While visiting Karluk Lake during 1926–30, Willis Rich saw numerous sticklebacks wherever he traveled, not only in the littoral, but also in the lake's open waters far from shore. Sticklebacks also littered the ground around gull and tern nests on Gull Island:

> [Gull Island, Karluk Lake, 20 July 1926] The small fish seen breaking the surface of the lake . . . are sticklebacks—3 spined—and they must be extremely numerous. The gulls and terns especially apparently feed on these sticklebacks as they can be found about the nests of these birds.[17]

He collected a "multitude" of sticklebacks in a 30 m seine at Camp Island on 15 August 1926 and made similar catches wherever he tried the net in Karluk Lake. The following year he saw large schools of young sticklebacks around Camp Island:

> [Karluk Lake, 11 July 1927] Small sticklebacks are extremely numerous all along the shore. Along the shore of the island near camp there have been literally thousands in small compact schools in the shallow water. Most of them are about 1" in length, though there are a few larger ones scattered among these. I assume that these small ones are from the eggs laid down last year.[18]

Sticklebacks continued to be abundant in 1930, including one seine haul of "only about 2,000 sticklebacks" from near Moraine Creek.[19] Rich seldom estimated the stickleback numbers in the seine hauls; instead, he noted their large abundance with descriptive terms such as "the usual multitude," "of course a lot," and "plenty." In fact, sticklebacks were then so

[15] See footnote 6.

[16] Mary Faustini, FWS biologist, saw the stickleback mass migration in the O'Malley River in 1997. Mary Faustini, Kenai, AK, personal commun. with Richard L. Bottorff, 1998.

[17] Rich, Willis H. 1926–1930 notebooks. Location of original notebooks unknown; copies at NARA, Anchorage, AK, and ABL Library, Auke Bay, AK.

[18] See footnote 17.

[19] Rich could not beach seine at Karluk Lake in 1929 because a trapper had used the USBF Camp Island cabin the previous winter and departed with the seine corks.

abundant that it was noteworthy when a seine caught only a few of these small fishes. Rich was the first biologist to record that sticklebacks and their eggs were important mid summer foods of charr at Karluk Lake.[20] When he inspected the stomach contents of charr caught near Camp Island in July–August 1927 and July 1930, he was surprised to find that stickleback eggs and adults were the most common foods. For example, one charr had eaten about 2,000 stickleback eggs and another large charr (460 mm) contained 12 adult sticklebacks (90–100 mm).

Barnaby spent much time observing the fishes of Karluk Lake during 1930–37 and regularly seined for young sockeye at many sites.[21] Typically, each seine harvested hundreds or thousands of sticklebacks, and occasionally more than 10,000. He believed that stickleback populations fluctuated widely from year to year and found them more abundant in 1930 than in 1931. On 22 July 1931, he saw about 100 dead sticklebacks along the upper O'Malley River, but he seemed unaware that they were post-spawning adults. Oddly, Barnaby and Rich, in spite of their many biological interests and keen field observations, never mentioned the mass migrations of sticklebacks into the two tributary lakes. In 1935–36 Barnaby confirmed Rich's findings that charr ate many stickleback eggs, young, and adults at Karluk Lake in June–July. Since he chiefly collected in Karluk Lake proper, these food habit results pertained mostly to Arctic charr and not to Dolly Varden. When Barnaby examined the stomach contents of sticklebacks in July 1935, he found cladocera and copepod zooplankton, plus a few stickleback eggs.

1939–41: Sticklebacks as Food for Charr

During 1939–41 DeLacy (1941) and Morton (1982) studied charr food habits in the Karluk ecosystem, examining more than 5,000 charr stomachs from many habitats. Arctic charr, which mainly inhabited Karluk Lake, fed heavily on stickleback eggs, young, and adults in June–July, but Dolly Varden seldom preyed on sticklebacks. Because of these results, DeLacy and Morton proposed a new theory for the stickleback-sockeye interaction. Originally, sticklebacks and juvenile sockeye were assumed to intensely compete for zooplankton foods, but now it seemed possible that abundant stickleback populations might partially protect young sockeye from charr predation. DeLacy and Morton argued that if stickleback numbers were reduced by either control methods or natural fluctuations, charr predation might increase on juvenile sockeye. Or, if charr numbers were reduced, stickleback populations might increase and intensify their competition with juvenile sockeye. Even so, without accurate population and ecological studies of sticklebacks, juvenile sockeye, and charr, it was difficult to know the ultimate outcome of any population control program.

Morton suggested that early attempts to control charr at Karluk Lake may have been counterproductive, leading to larger stickleback populations:

> [Karluk Lake, 1939–1941] I will venture to say there are 1000 sticklebacks present for each young red salmon inhabiting the lake based purely upon my own observations the past three summers there. I still maintain that Hoffstad's removal of large numbers of charrs (50,000 per season he told me) mostly of the lake type no doubt, in 1929 or 30 or thereabouts was probably followed by abnormally successful broods of sticklebacks . . . say for '30, '31, and '32 . . . and that they have maintained these numbers at recent years at the expense of the young red salmon whose food they eat.[22]

Although little evidence exists that 50,000 charr were annually removed from Karluk Lake in the 1920s–1930s, it does remains a possibility for a few of these years. In fact, the USBF discussed such plans for the 1927 field season.[23] Thus, charr removal at Karluk may have increased stickleback populations and intensified competition with juvenile sockeye during 1927–30.

While studying charr, DeLacy and Morton incidentally caught many sticklebacks in their sampling gear from the littoral and limnetic zones of Karluk Lake. To get a relative measure of stickleback abundance during 1939–41, they examined the catches of 60 fyke-net sets in the lake's littoral. On average, for every young sockeye captured, they caught 5 Dolly Varden, 27 Arctic charr, and 1,055 sticklebacks (Morton, 1982). These astonishing results demonstrated that sticklebacks were then, by far, the most abundant fish in Karluk Lake.

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[20] See footnote 17. Although Rich called these predatory fishes Dolly Varden, they most likely were Arctic charr.

[21] Barnaby, J. Thomas. 1930–1937 notebooks. Located at NARA, Anchorage, AK.

[22] Morton, Mark. c. 1942. No title. Unpubl. report 3 p. Located at NARA, Anchorage, AK.

[23] Letter (3 December 1926) from Howard H. Hungerford, Warden, Alaska Service, USBF, Seattle, WA, to Dennis Winn, Agent, USBF, Seattle, WA. Located at NARA, Anchorage, AK.

1940s: Recommendations for Stickleback-Juvenile Sockeye Study

When Shuman, the leader of FWS research at Karluk during 1943–49, periodically visited the lake in 1943, he found enormous numbers of sticklebacks. Traveling north along the lake's eastern shoreline from Thumb River to Grove Point in July he declared that "sticklebacks were observed by countless numbers—certainly several million" and felt this would be a good place to study these fishes or attempt to control them.[24] But fewer sticklebacks occurred along the lake's western shoreline, though he was unsure why.

After observing vast multitudes of sticklebacks at Karluk Lake for several years, Shuman believed they competed with young sockeye and speculated that reduced charr populations of recent years had released sticklebacks from intense predation and caused their numbers to expand. As evidence he claimed that previous researchers at Karluk Lake had often mentioned its abundant charr, but seldom recorded plentiful sticklebacks. From his own observations, charr seemed to be scarce at the lake in the mid 1940s, though he was uncertain if past bounty programs or natural fluctuations were responsible. Although little data existed on the resident fish populations of Karluk Lake, Shuman believed a causal inverse relationship existed between charr and stickleback numbers.[25]

In 1945 Shuman prepared a manuscript that analyzed the escapements and returns of Karluk River sockeye salmon and sent it to Willis Rich for review. Because Rich believed that nutrient depletion of the lake had caused the declining sockeye runs, he recommended that Shuman study the lake's limnology and the interaction between juvenile sockeye, sticklebacks, and charr:

> [Concerning the research program at Karluk Lake] If the experiment of artificial fertilization of Karluk Lake is to be tried it should only be in connection with an expanded and rounded out program of study. The present investigation of the effects of known escapements is, of course, essential; the limnological studies should be made more complete; the study of predation and competition should be started and vigorously pressed. . . . From what Shuman tells us it appears to both Barnaby and me that sticklebacks (presumably competitors) have tremendously increased in Karluk Lake during the nearly 20 years since I have been there. At the same time Dolly Varden have apparently decreased markedly—perhaps due in part to the campaign to eliminate these predators. But here the plot thickens because the chars feed heavily on young sticklebacks and stickleback eggs and may do more good by keeping down the population of these competitors than they do harm as predators on the young salmon.
>
> Need for study of competition and predation in the lakes—stickleback—Dolly Varden—red salmon "biome".[26]

Shuman accepted many of Rich's ideas and pursued limnological and limited stickleback studies in 1947. To assist these studies, Rich revisited Karluk Lake in 1947 to see if stickleback numbers had increased since his work of the 1920s. The initial consensus was that they were more profuse in 1947, but upon reflection there seemed to be little difference in numbers:

> [Karluk Lake, 4 August 1947] Rich believes stickleback more numerous than in 20's .. . . Rich stopped on way to Camp Island to check on sticklebacks. Claims a few more than what was present during late 20's.
>
> [Karluk Lake] In 1947 or 1948 Dr. Willis Rich visited Dick Shuman and I at Karluk. Dr. Rich spent several days with us going over the lake and visiting several of the tributary streams. Dick was of the opinion that sticklebacks may have been more numerous at that time, but Dr. Rich did not think they were any more abundant than during early years, likewise Dolly Varden and Charrs. Hence one wonders about the feasibility of reducing the populations of these two species as for all we know they are as numerous now as ever.[27]

Besides the abundant sticklebacks in Karluk Lake, they were also common in the upper river as was revealed in an unusual event. In September 1943, as Shuman tended the Portage weir, the rain-swollen river floated huge masses of decayed aquatic plants against the weir. Entangled in the plant masses were hundreds of dead sticklebacks but no young salmon. Shuman claimed that thousands of sticklebacks had been destroyed by this incident.[28]

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[24] Shuman, Richard F. 1943 notebook. Located at NARA, Anchorage, AK.

[25] Shuman, Richard F. 1951. Trends in abundance of Karluk River red salmon with a discussion of ecological factors. Manuscript prepared for Fishery Bulletin 71, Volume 52. Unpubl. report. 56 p. Located at ABL Office Files, Auke Bay, AK.

[26] 1) Letter (11 May 1946) from Willis H. Rich, Consultant, Salmon Fishery Investigations, to Elmer Higgins, Chief, Division of Fishery Biology, FWS, Washington, DC.
2) Letter (16 August 1946) from Willis H. Rich, Consultant, Salmon Fisheries Investigations, Stanford University, to R. F. Shuman, FWS, Seattle. Both located at NARA, Anchorage, AK.

[27] 1) Richard F. Shuman 1947 notebook (4 August) and Philip R. Nelson 1947 notebook (4 August).
2) Letter (11 June 1957) from [Phil Nelson ?], FWS, Annapolis, MD, to John Owen, FWS, c/o Roy Lindsley, Kodiak, AK. All located at NARA, Anchorage, AK.

[28] Shuman, Richard F. 1943 notebook. Located at NARA, Anchorage, AK.

Fisheries Research Institute biologist Donald Bevan examining the masses of threespine sticklebacks in a beach seine, Karluk Lake, 1950s. (Charles E. Walker, Sechelt, BC)

1948–56: Nelson and Greenbank Study Stickleback Life History

Nelson first studied the life history of sticklebacks at Karluk Lake during 1948–49 and 1951. With Greenbank's help, he continued these studies in 1956 and expanded them to include nearby Bare Lake (Greenbank and Nelson, 1959). Although accurate estimates were lacking for Karluk Lake's fish populations, sticklebacks were thought to be the most abundant fish in the lake, but there were large fluctuations in their numbers from year to year. Typically, each beach seine haul (using a 21 m net) caught 300–1,500 sticklebacks during the summer, but captured few in October–November once these fish had moved offshore or into deeper water.[29] Although a pioneering effort, Nelson and Greenbank's study had a serious sampling flaw—they only collected sticklebacks from a few littoral sites at Karluk Lake and excluded the open-water limnetic zone. Their study also gave little indication of the controlling factors on stickleback numbers and the intensity of competition with juvenile sockeye:

> Years ago a rather comprehensive seining and trapping program of Dolly Varden and Charr was undertaken at Karluk. Unfortunately no measure was made of the reduction in the Charr and Dolly Varden population. There was some talk that the stickleback population had increased, however, no actual measurement was made that I know of, only casual observations. Personally I don't know what would happen if the Charr and Dolly Varden population was drastically reduced. Perhaps an increase in Sticklebacks would result which would be equally detrimental to red salmon as they are competitors for food. Of course we do not know how important a competitor they are.[30]

[29] Freeman, Arthur. 1948 notebook. Original notebook in personal papers of Arthur Freeman, Indianapolis, IN.

1950s: Stickleback Observations by Walker and Bevan

FRI biologists Charles Walker and Donald Bevan gathered data on stickleback abundance at Karluk Lake during 1950–54 with a regular sampling program using beach seines (3–61 m length).[31] They primarily tried to catch young sockeye, but most seine hauls netted sticklebacks too numerous to count. To quantify these multitudes, they measured the volume of sticklebacks captured and converted this to numbers (171 fish per liter for large sticklebacks; 3,914 fish per liter for small sticklebacks). Overwhelmingly, sticklebacks were the most abundant fish in their collections at all lake habitats and times.[32]

To get a relative measure of stickleback and juvenile sockeye abundance in Karluk Lake, Walker and Bevan compared their beach seine samples for a standard one-month period starting in the third week of July. They chose this period since sockeye smolts had

[30] Letter (11 June 1957) from [Phil Nelson ?], FWS, Annapolis, MD, to John Owen, FWS, c/o Roy Lindsley, Kodiak, AK. Located at NARA, Anchorage, AK.

[31] See footnote 9. To sample the resident fishes of Karluk Lake they also used traps, trawls, and tow nets, besides beach seines. Walker prepared a short report of his Karluk stickleback observations: Walker, Charles E. 1954. Comments on the life history of Karluk Lake stickleback (*Gasterosteus aculeatus*). Kodiak Island Research, FRI, University of Washington, Seattle, WA. Unpubl. report. Not located, but probably exists in FRI Archives, University of Washington, Seattle.

[32] Walker, Charles E., and Donald E. Bevan. ca. 1968. Factors possibly contributing to the condition of the Karluk sockeye salmon run. Unpubl. handwritten report. 18 p. Located in FRI Archives, University of Washington, Seattle.

departed the lake, emerging sockeye fry had entered the lake, stickleback adults had spawned and redistributed throughout the lake, and newly hatched sticklebacks would reach swimming stage in late August. On average for this period, for every juvenile sockeye caught, 25 sticklebacks were caught in 1950 (38 littoral seine hauls) and 50 sticklebacks were caught in 1951 (61 seine hauls). They roughly estimated that 300,000,000 sticklebacks with a total weight of 302,550 kg inhabited Karluk Lake, far in excess of the estimated 45,360 kg of juvenile sockeye. Since sticklebacks made up more than 80% by weight of the plankton-eating fishes, Walker and Bevan concluded that "the stickleback population in Karluk Lake outnumbers and outweighs the sockeye salmon and may be a serious competitor for food to juvenile salmon."

1960s: Limnetic Sampling of Sticklebacks

BCF biologists regularly sampled the fishes of Karluk Lake in 1961–62 using 30 m beach seines in the littoral and, for the first time, tow nets in the limnetic zone (Ellis, 1963; Gard and Drucker, 1963).[33] As with all previous studies, sticklebacks far outnumbered young sockeye in both habitats. Sticklebacks accounted for over 90% of the beach seine and tow net catches in 1962, while juvenile sockeye made up only 5–6%. Without a doubt, sticklebacks were the most abundant fish in Karluk Lake, and the potential for competition between the two species appeared to be great since both species reached peak abundance in the littoral in July and in the limnetic zone in August. Additional studies of sticklebacks were not pursued by the BCF after 1962 and they ended all field work at Karluk Lake in 1969 as the ADFG began its research.

1970s: Stickleback Observations by Blackett at Thumb Lake and River

After several years of preliminary studies at Karluk Lake, in 1970 the ADFG developed a multi-year plan to rehabilitate the sockeye salmon run of the Thumb River, a major spawning tributary to Karluk Lake. To do this, sockeye fry would be produced within in-stream incubators in the Upper Thumb River. Thumb Lake would be improved as initial rearing habitat for these young sockeye, this shallow lake being an ideal environment for newly emerged fry before they moved downriver to Karluk Lake. A control structure was planned on the Lower Thumb River to block predator and competitor fishes from entering Thumb Lake, but to still allow adult and juvenile sockeye to freely pursue their natural migrations. The ADFG intended to use fish toxicants to remove existing predators and competitors from the Thumb system, with sticklebacks being the main competitors to be eliminated.

To further examine the project's feasibility, ADFG biologist Blackett (1973) studied Karluk Lake and the Thumb River in 1971–72. He installed a weir across the Lower Thumb River to monitor salmon movements in 1971, but he soon witnessed the mass stickleback migration:

> [Lower Thumb River, 1971] In 1971, there was a massive migration of millions of three-spined stickleback from Karluk Lake into Thumb Lake. Observations of the migration were recorded incidental to fry indexing in Thumb River. After June 10, problems began developing with stickleback moving upstream and then drifting downstream and clogging the index nets. It was not uncommon to have 3,000 to 4,000 stickleback caught in a net in less than a day. The upstream migration became more intense and on June 20, the river behind the weir was black with stickleback so thick that the stream bottom could not be seen. Concentrations of stickleback were also schooled in Karluk Lake off the river mouth. All of the stickleback examined were sexually mature and considered to be in spawning migration. Movement of sticklebacks was observed upstream into the shallow outlet of Thumb Lake and into Salmon Creek. Fewer stickleback were moving upstream by the end of June and early July and concentrations in the river were less dense. A similar mass migration was not observed in 1972.

It is unclear if Blackett expected this stickleback migration, but he was impressed by the hordes moving upstream and the possibility that sticklebacks might reduce the growth of young sockeye:

> A massive abundance of stickleback is present in Karluk and Thumb Lakes. The concentrations observed far exceed stickleback observations in other major lakes of Kodiak Island. It is not known if these competitor species were also abundant in early years or if they increased as the sockeye decreased and lost dominance in lake rearing areas. Since the three-spine stickleback subsists on the same planktonic crustacea and fre-

[33] Drucker, Benson. ca. 1965. Age, size, abundance and distribution of juvenile sockeye salmon (*Oncorhynchus nerka*) at Karluk Lake, Alaska, 1961–1962. BCF, ABL, Auke Bay, AK. Unpubl. report. 30 p. Located at NARA, Anchorage, AK.

quents the same lake areas—inshore waters during early fry stage, and the pelagic region in fingerling and yearling stages—it must have a devastating affect upon growth and survival of young sockeye in the same waters. The stickleback population of Karluk Lake most certainly cannot be ignored as a factor possibly limiting or depressing sockeye productivity.

Although the ADFG cancelled the proposed control structure and poisoning program, they rehabilitated the Thumb River sockeye run during 1978–86 by planting millions of eyed-eggs and fry into the upper river.

After studying Karluk Lake for most of the 1970s, many ADFG biologists agreed that sticklebacks may compete with juvenile sockeye and hinder attempts to rehabilitate the salmon runs. Apparently during this period they examined the food habits of sticklebacks and juvenile sockeye to document the amount of dietary overlap, but a detailed study of the possible competition was lacking. Surprisingly, although food competition seems likely between sticklebacks and juvenile sockeye, little comparative data on the diets of these species exist in the historical literature of Karluk.

1980s: Stickleback Growth, Abundance, and Movements

USFWS biologists conducted several studies at Karluk Lake during 1982–88 to evaluate the ADFG's ongoing rehabilitation efforts, which then included restoration of the Thumb River sockeye run and artificial fertilization of the main lake.[34] One USFWS study explored the stickleback-juvenile sockeye interaction. During 1982–84 they measured the abundance and distribution of both species in the littoral using beach seines and fyke nets.[35] Since this sampling effort bypassed the limnetic zone, during 1985–88 they measured stickleback age, growth, and distribution in Karluk, Thumb, and O'Malley lakes using beach seines (31 m) in the littoral and tow nets in the limnetic zone.[36] Their sampling efforts were comprehensive; collections came from 15 beach seine sites and many nighttime tow-net transects in all three basins of Karluk Lake.

This multi-year sampling program gave biologists new insights into stickleback abundance, seasonal habitats, age, growth, response to environmental changes, and potential competition with juvenile sockeye. Sticklebacks were the most abundant fish in Karluk Lake during 1982–88, and it was thought that their numbers may have increased over the past 20–40 years. Sticklebacks accounted for over 95% of littoral fishes during 1982–84, while juvenile sockeye made up only 1.1–3.5%. On average, fyke nets caught 2,840 sticklebacks for every juvenile sockeye trapped. Similar results occurred during 1985–88, with each beach seine typically netting several thousand sticklebacks and occasionally over 30,000. On a yearly average, beach seines caught more than 10 sticklebacks (range 12.9–37.8) for every juvenile sockeye caught in Karluk Lake. The stickleback-sockeye proportions in Thumb and O'Malley lakes were either similar to those in Karluk Lake or substantially higher (range, 6.4–137.0). Sticklebacks also dominated the limnetic tow net samples, with 5–15 sticklebacks caught for every juvenile sockeye. Because young sockeye avoided the tow nets better than sticklebacks did, the limnetic samples tended to inflate the apparent dominance of sticklebacks in the open waters of Karluk Lake.

Stickleback ages and growth were also determined from this sampling effort using length-frequency diagrams; ages were initially confirmed by counting otolith annuli. Five age groups existed in the summer: age-0, 1, 2, 3, and 4. Sticklebacks usually reached sexual maturity at age-3, but a few survived to age-4 and fast-growing individuals reached sexual maturity at age-2. These ages were greater by one year than those previ-

[34] USFWS biologists included Richard L. Wilmot, James E. Finn, John D. McIntyre, Robert A. Olson, Reginald R. Reisenbichler, Terry Terrell, and others.

[35] 1) Wilmot, Richard L., Carl V. Burger, David B. Wangaard, James W. Terrell, and Robert M. Lichorat. 1983. Karluk Lake studies, progress report. USFWS, Alaska Field Station, National Fishery Research Center, Anchorage, AK (July 1983). Unpubl. report. Copy from Richard L. Wilmot, ABL, Auke Bay, AK.
2) USFWS. 1985. Karluk Lake sockeye salmon studies 1984. Part I: Competition, predation, and lake fertility. Part II: Karluk Lake smolt outmigration—1984. Draft. USFWS, Seattle National Fishery Research Center, Alaska Field Station (January 1985). Unpubl. report. 39 p. Copies located at ADFG Office Files, Kodiak, AK, and ARLIS, Anchorage, AK.

[36] 1) Olson, Robert A., and Richard L. Wilmot. 1989. Karluk Lake sockeye salmon and threespine stickleback studies (1982 to 1988). USFWS, Region 8, Alaska Fish and Wildlife Research Center, Anchorage (29 June 1989). Unpubl. report. 56 p. Copy from Richard L. Wilmot, ABL, Auke Bay, AK.
2) Wilmot, R. L., R. A. Olson, R. R. Reisenbichler, J. D. McIntyre, and J. E. Finn. ca. 1989. Effects of competition with threespine stickleback (*Gasterosteus aculeatus*) on growth of age-0 sockeye salmon (*Oncorhynchus nerka*) in Karluk Lake, Alaska. USFWS, Alaska Fish and Wildlife Research Center, Anchorage. Unpubl. report. 20 p. Copy from Jim Finn, FWS, Anchorage, AK.

ously reported by Greenbank and Nelson (1959), who failed to find age-0 and age-4 fish (and caught few age-3 fish), possibly because they collected from only one littoral site and no limnetic sites.

Stickleback abundance and distribution showed distinct seasonal patterns within the three lakes. From late May to early June, sexually mature adults (typically age-3) left Karluk Lake's limnetic waters and accumulated in the littoral near Thumb and O'Malley rivers. These were males in spawning coloration and females ripe with eggs. After ascending the two rivers in a mass migration to Thumb and O'Malley lakes, they spawned in thick beds of aquatic plants (*Potamogeton, Elodea,* and *Ulothrix*) growing in the shallow waters. Many mature sticklebacks inhabited both tributary lakes in June, followed by dead spawned-out adults found along the shorelines in July. Some sticklebacks spawned in a few suitable habitats scattered around Karluk Lake, but its steep rocky shoreline was not favorable for large aquatic plant beds to develop. Young sticklebacks of 5 mm length hatched in late summer and these age-0 fish inhabited the aquatic plants of tributary lakes in August–October. Most sticklebacks reared in Karluk Lake after their first year, first inhabiting its littoral and then with age moving into its limnetic zone. Immature age-1 and -2 sticklebacks inhabited Karluk Lake's littoral in spring and summer, and then the older group gradually moved into limnetic waters as summer progressed and as age-3 fish declined in abundance. The younger sticklebacks inhabited the littoral through October, but then all fishes became scarce near shore as colder waters forced them into deeper waters.

In summary, Karluk's sticklebacks cycled through a series of different habitats as they aged. Eggs and age-0 fish occurred in aquatic plant beds of tributary lakes. Age-1 and -2 fish occurred in Karluk Lake's littoral. Age-3 and -4 fish inhabited Karluk Lake's limnetic zone. Spawning adults returned to tributary lakes in a mass migration. These vibrant seasonal exchanges between habitats suggested that littoral and limnetic sticklebacks were genetically similar, a fact confirmed by electrophoretic studies.[37] Prior to the 1982–88 research, sticklebacks in Karluk Lake were thought to be rather sedentary fish. These new studies revealed a complex and dynamic aspect of the Karluk Lake ecosystem: the distinct seasonal movements of sticklebacks between several habitats as they aged and grew. In some aspects, Karluk's sticklebacks have a life cycle paralleling, in miniature, that of sockeye salmon.

Juvenile sockeye abundance and distribution also had distinct seasonal patterns. Age-0 sockeye inhabited Karluk Lake's littoral from late May to late July and reached peak abundance there in mid June. They then moved into the lake's limnetic waters and seldom inhabited the near shore zone after early August. Since sticklebacks and young sockeye both inhabited the littoral in June–July, these months may be a critical period of competition between the two species.

1980s: Stickleback Competition with Sockeye Salmon Juveniles

USFWS biologists conducted a field experiment at Karluk Lake during 1985–88 to test if adult sticklebacks competed with age-0 sockeye salmon.[38] To do this, they experimentally reduced the population density of adult sticklebacks in O'Malley Lake, while the natural stickleback population in Thumb Lake served as a control. They then compared the growth rates of age-0 sockeye in these two tributary lakes to find evidence of food limitation and competition.

For this field experiment, a small barrier dam was built across the O'Malley River to prevent sexually mature sticklebacks from migrating into O'Malley Lake during 1985–87, but the low dam still allowed free upstream passage to adult sockeye. The dam caused adult sticklebacks to accumulate just downstream (masses of 100,000s of fish), and these concentrations attracted opportunistic-feeding bears, foxes, and birds. The barrier excluded age-3 sticklebacks from O'Malley Lake, where in previous years these fish were common during the spawning season. Sticklebacks were reduced to about half their original density in O'Malley Lake. Thus, the field trial altered the age structure and reduced the density of sticklebacks in O'Malley Lake for three years. When the barrier dam was removed in 1988, age-3 sticklebacks once again freely migrated to the lake.

By excluding age-3 adults from O'Malley Lake, resident young sticklebacks (age-1 and -2) increased their growth rate and reached larger sizes than similarly aged fish in Karluk and Thumb lakes. Age-2 sticklebacks in O'Malley Lake reached sizes equal to age-3 fish in Karluk Lake and some of these younger fish attained sexual maturity. Because of the reduced densities, juvenile sticklebacks remained in O'Malley Lake

[37] Richard Wilmot, Auke Bay, AK, personal commun. with Richard L. Bottorff, 1998.

[38] See footnote 36.

Barrier placed in the O'Malley River to stop the upstream migration of sticklebacks into O'Malley Lake, 1985-87. (Jim Finn, Anchorage, AK)

Threespine stickleback masses concentrated below the O'Malley River barrier, 1985-87. (Jim Finn, Anchorage, AK)

rather than following their past behavior of moving downstream to rear in Karluk Lake. This exclusion experiment showed that resident sticklebacks quickly responded to environmental changes, growing faster, reaching sexual maturity one year earlier than normal, and rapidly filling the open niche in O'Malley Lake. Yet, since pre-exclusion baseline studies of stickleback age and growth were lacking, some caution is justified about these results. The growth of young sticklebacks varied widely among the three lakes during the four study years; this result reinforced the anecdotal evidence that stickleback numbers fluctuated from year to year.

When the growth rates of age-0 sockeye in the experimental (O'Malley) and control (Thumb) lakes were compared, adult sticklebacks apparently competed with age-0 sockeye and reduced their growth rate. That is, by reducing the adult stickleback density in O'Malley Lake, the growth rate of age-0 sockeye increased above that of the control lake. Further, reduced stickleback densities caused density-independent factors to control age-0 sockeye growth in O'Malley Lake, not the typical density-dependent response found in Thumb and many other sockeye salmon lakes in Alaska. Age-0 sockeye reached weights of 1–2 g in both experimental and control lakes at the end of the growing season, much less than the 3–8 g predicted from a growth model that assumed unlimited food. This indicated that juvenile sockeye growth was food limited and that competition was important. Yet, the biologists cautioned that attempts to control stickleback numbers by restricting their access to tributary spawning lakes may ultimately be futile, though temporarily effective, since increased growth of resident sticklebacks quickly offset the initially depleted population.

In summary, USFWS biologists discovered new information during 1982–88 about stickleback life history and stickleback-sockeye interactions in the Karluk ecosystem. They showed that stickleback populations were dynamic, that these fish made distinct

movements between habitats and had the ability to rapidly expand their numbers. For the first time, biologists tested the assumption that sticklebacks competed with juvenile sockeye for food. Sticklebacks apparently reduced the growth of age-0 sockeye and may have hindered the recovery of depleted sockeye runs at Karluk. Whether sticklebacks competed with older and larger juvenile sockeye remained untested. Although additional research is needed on the stickleback-sockeye interaction, these studies were significant accomplishments.

To evaluate the competition between sticklebacks and juvenile sockeye, it is essential to know the food habits of both species and the amount of food overlap that exists in their diets. The USFWS planned to study the food habits of both species during 1982–88, but this work was never completed.[39] Apparently in 1984 the ADFG conducted preliminary food studies of limnetic sticklebacks and young sockeye in Karluk Lake.[40] Reportedly, both species ate the same zooplankton foods, but sticklebacks ate smaller-sized prey than did young sockeye. Despite the importance of this topic for understanding stickleback-sockeye interactions, we found little food habit data for sticklebacks and young sockeye in the published and unpublished literature of Karluk; this major research deficiency should be addressed. In addition, knowing how sticklebacks and young sockeye use the limnetic zone of Karluk Lake by basin location, depth, season, and diel cycle may reveal the scope and intensity of competition (Kyle 1990).

1980s–90s: Hydroacoustic Estimates of Stickleback Populations

Using new technology, ADFG biologists estimated the abundance and distribution of Karluk Lake's limnetic fishes during 1983–97. Each September they used hydroacoustic methods and tow nets to estimate these fish populations, which were primarily composed of sticklebacks and juvenile sockeye salmon (Kyle, 1990; Schrof et al., 2000). Similar to the USFWS results, tow nets caught about 10 sticklebacks (range, 2.1–83.5) for every juvenile sockeye, and the stickleback-sockeye ratio increased between spring and autumn. The ADFG did not estimate the stickleback population from the hydroacoustic and tow net data, but they did calculate the total fish population and juvenile sockeye numbers in the lake. The difference between the total population and sockeye numbers gives a very rough index of the sticklebacks present. According to this index, stickleback populations averaged 45,000,000 fish during this period (range, 13,000,000–76,000,000), with large year-to-year changes in abundance (Fig. 8-1). When Karluk Lake was artificially fertilized during 1986–90, stickleback populations averaged 58,000,000 fish.

Though artificial enrichment and larger sockeye escapements possibly enhanced the lake's fertility and stickleback numbers during 1983–97, it was unclear if stickleback and juvenile sockeye populations varied inversely, as might be expected with a competitive interaction. Instead, stickleback populations appeared to vary directly with sockeye escapements (Fig. 8-1), suggesting that stickleback numbers were influenced by the inputs of fertilizers and salmon-carcass nutrients. If so, the long-term decline of sockeye salmon runs at Karluk during 1890–1985, and the subsequent reduced lake fertility, may have simultaneously decreased both stickleback and juvenile sockeye populations. This seldom considered possibility directly opposes the theory that sticklebacks expanded their abundance and filled the niche of juvenile sockeye as the salmon runs declined.

2000–2003: *Bosmina* Abundance and Stickleback Competition

Recent studies of sediment cores from Karluk Lake have shown a direct relationship between the abundance of the zooplankter *Bosmina longirostris* and sockeye salmon escapement over the past 500 years (Finney et al., 2000; Sweetman and Finney, 2003). Because juvenile sockeye actively select *Bosmina* as a food item in Karluk Lake (Table 4-14), an inverse relationship might be expected between predator and prey abundance. Such a relationship seems plausible since sticklebacks also prey on these cladocerans. Yet lake sediments record that *Bosmina* abundance was controlled by salmon-derived nutrient loading, not by fish predation, making it unlikely that sticklebacks and juvenile sockeye intensely competed for this pre-

[39] Samples of sticklebacks and juvenile sockeye collected in beach seines and tow nets (1982–88) were preserved for future analysis of food habits. These fish samples may still exist in storage in Juneau, AK (1997).

[40] We did not locate these food habits data in any published or unpublished report, but found a brief mention of this work, possibly done by the ADFG. USFWS. 1985. Karluk Lake sockeye salmon studies 1984. Part I: Competition, predation, and lake fertility. Part II: Karluk Lake smolt outmigration—1984. Draft. USFWS, Seattle National Fishery Research Center, Alaska Field Station. (January 1985). Unpubl. report. 39 p. Copies located at ADFG Office Files, Kodiak, AK, and ARLIS, Anchorage, AK.

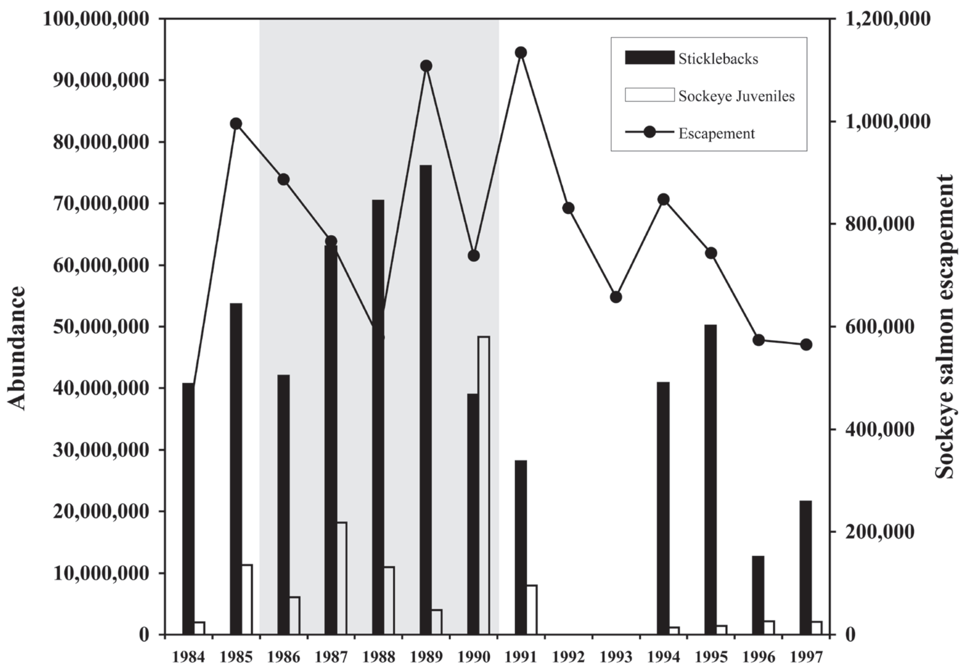


Figure 8-1. Estimated stickleback and juvenile sockeye populations in Karluk Lake each September, 1984-97 (histogram bars) and sockeye salmon escapements (●). Abundance data were derived from Schrof et al. (2000) and escapement data were from ADFG Karluk River weir counts. The shaded area shows the Karluk Lake fertilization period (1986-90).

ferred zooplankton food. Of the other common macrozooplankton in Karluk Lake (*Cyclops, Daphnia,* and *Diaptomus*), juvenile sockeye tended to avoid these as food items unless the copepods were ovigerous. It remains unknown whether sticklebacks and juvenile sockeye compete for these other macrozooplankton; this emphasizes once again the critical need for food studies of these two fish species.

Summary

Sticklebacks have a remarkably dynamic life cycle in the Karluk ecosystem. Each life stage moves between distinct habitats within the lake and its tributaries. The mass spawning migration of adult sticklebacks up the Thumb and O'Malley rivers is notable. Sticklebacks have always been abundant in Karluk Lake, but the factors controlling their numbers remain unknown. It is unclear if populations expanded into the open niche created by the long-term decline of the sockeye runs, or, conversely, diminished in recent years as sockeye numbers rebounded. Field observations and recent population estimates indicate that stickleback abundance varies considerably from year to year. Karluk's sticklebacks rapidly respond to environmental changes and may benefit, along with young sockeye, from salmon-carcass nutrients added to the lake.

Sticklebacks and age-0 juvenile sockeye apparently compete for food in O'Malley Lake, though further research is needed of this interaction in Karluk Lake, including studies of their food habits, habitat use, and competition with other age classes of young sockeye. Arctic charr, birds, and mammals prey on sticklebacks at Karluk Lake in the summer, but how this affects their population size is unknown. No evidence exists that Karluk's sticklebacks prey on sockeye juveniles or eggs; juvenile sockeye occasionally prey on sticklebacks. Abundant stickleback populations may buffer juvenile sockeye from charr predation, but the validity of this idea is unexplored. As found for Karluk's sockeye salmon, the answers to questions about sticklebacks must include a wide range of environmental conditions, not extrapolations from a few isolated observations.

Because the interaction between sticklebacks and juvenile sockeye remains largely unexplored at Karluk Lake, opinions about the relationship are guided by anecdotal evidence, field collections, scattered observations, and intuition. These disparate sources suggest that sticklebacks and young sockeye may compete for

resources in Karluk Lake since they have apparent similarities in size, habitats, and foods. Further, the huge abundance of sticklebacks in Karluk Lake raises suspicions that the vast numbers must somehow adversely impact young sockeye. Nevertheless, these two species have coexisted in the Karluk ecosystem for many millennia, and it seems reasonable to assume they have evolved adaptations to minimize competition. When these two species are compared, sockeye salmon have major impacts on the entire Karluk ecosystem by their carcass-nutrient inputs, while sticklebacks appear to have few system-wide effects. From an evolutionary perspective, it seems unlikely that the unique life cycle features of sockeye salmon would persist if sticklebacks were such superior competitors that they co-opted the lake fertility benefits given by the salmon.

CHAPTER 9

Dolly Varden and Arctic Charr Predation

Charr—are they aquatic wolves or benign sheep?

Karluk Lake has abundant populations of two charr species: Dolly Varden, *Salvelinus malma,* and Arctic charr, *Salvelinus alpinus.* These closely related charr have similar general appearances and for many years were thought to be the same species. As a consequence, for the first 60 years of Karluk's fisheries history (1880–1939), all charr were called Dolly Varden, though another common name used was "salmon trout." Yet some early biologists noticed dissimilarities in the charr at Karluk and judged the two forms to be races of one species. William Morton examined Karluk's charr in 1939 and found distinct variations in coloration, morphology, and parasites (Morton, 1942; DeLacy and Morton, 1943). The observed differences were sufficiently large to represent two species, the Dolly Varden and Arctic charr, a taxonomic distinction generally followed thereafter (McPhail, 1961). Other terms that have been used in the past for Karluk's Dolly Varden are "ocean charr" and "Pacific brook charr," while Arctic charr have been called "lake charr."

Once canneries began operating on Karluk Spit in 1882, and for many decades thereafter, it was an unquestioned fact that Dolly Varden voraciously ate sockeye salmon eggs and juveniles. This belief existed not only at Karluk, but for all of Alaska and the Pacific Coast. Dolly Varden predation was then thought to significantly deplete salmon runs and reduce commercial harvests, and such losses were often cited as a key reason why Karluk's sockeye salmon runs had experienced a long-term decline. Thus, throughout Karluk's fisheries research history, biologists have devoted considerable effort to understanding the interaction between charr and sockeye salmon.

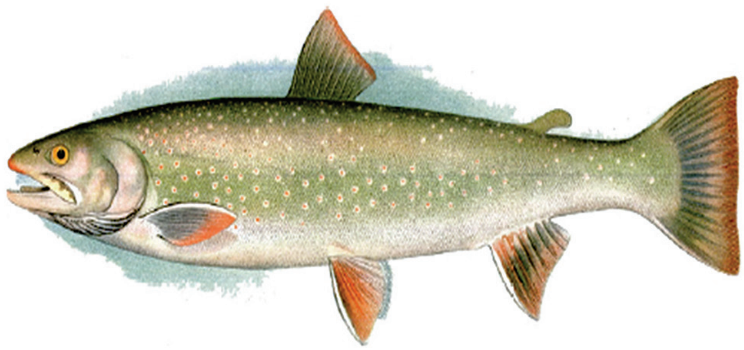
Definitions and General Life History

Before discussing Karluk's charr any further, the terms used in this chapter and the species involved must be defined. We use the term "Dolly Varden" for *S. malma* and "Arctic charr" for *S. alpinus.* When the term "charr" is used alone, it refers to both Dolly Varden and Arctic charr. These three names are needed because charr observations prior to 1939 at Karluk failed to clearly separate the two species, and the early literature must be used with caution. This is also true for some studies after 1939 since Dolly Varden and Arctic charr were not separated. Fortunately, it is often possible to infer the species being discussed in early studies because Dolly Varden and Arctic charr have distinct life history, habitat, and behavioral differences in the Karluk ecosystem.

Dolly Varden are anadromous, making annual migrations between Karluk Lake and the ocean; Arctic charr are non-migratory, remaining as lake residents throughout their life. Each year in late May and early June, many adult Dolly Varden migrate down the Karluk River to the sea, where they remain for about two months before ascending the river once again to Karluk Lake in mid July to September. In early autumn, adult Dolly Varden enter the larger tributaries of Karluk Lake in preparation for late fall and early winter spawning. These larger streams then serve as initial rearing habitat for juveniles of less than 150 mm length.

Arctic charr are almost exclusively restricted to Karluk Lake for their entire life cycle and only rarely occur in the upper Karluk River or the lower reaches of lake tributaries. Tagging studies of Arctic charr in Karluk Lake have documented that nearly all recoveries, even years later, come from the original tagging site (DeLacy, 1941). Arctic charr do not migrate to the ocean, and movements within the lake are limited. Beginning in late June as sockeye salmon arrive at their spawning sites, Arctic charr congregate near the mouths of lake tributaries to eat drifting salmon eggs and the flesh of decomposing salmon carcasses. In late fall and early winter, Arctic charr spawn in Karluk Lake, which then serves as rearing habitat for its juveniles.

Based on these specific differences, charr that occur in the ocean, Karluk River, and Karluk Lake tributaries usually are Dolly Varden, while charr that occur



Dolly Varden. (Drawing by Albertus H. Baldwin, from Evermann and Goldsborough, 1907.)

in Karluk Lake may be either Dolly Varden or Arctic charr. Since Dolly Varden normally vacate Karluk Lake in June–July, most lake charr discussed then are Arctic charr. Though habitat and life history data clarify the charr species of many early observations, some uncertainty remains for Karluk Lake fish.

Historic Efforts to Control Karluk's Charr Population

During the early years of the sockeye salmon fishery at Karluk, commercial harvests were large and canneries easily met their annual production goals, but once salmon runs began to diminish in the late 1890s and early 1900s, there was concern about the size of future runs and discussion of what factors were causing the decline. Of course, natural salmon predators, both real and perceived, received part of the blame for the smaller runs, and the list of animals that ravenously destroyed salmon continued to grow: bears, wolves, foxes, eagles, gulls, terns, mergansers, cormorants, kingfishers, loons, hair seals, sea lions, river otters, whales, charr, sculpins, salmon sharks, and others (Jones, 1915):

> [Alaska, 1914] It is necessary to study carefully all agencies, both natural and otherwise, tending to deplete the supply of salmon and other food fishes in the waters of Alaska, and to apply as far as possible proper remedial measures. Those engaged in the great fishing industry say the blame for the diminished numbers of salmon is due largely to natural enemies... These enemies undoubtedly destroy enormous numbers of salmon and their eggs. But this condition has gone on for years, and would continue without serious detriment to the supply if it were not for the added drain resulting from heavy fishing now carried on in Alaska waters. It is evident from close observation that man has had much to do with the waning supply of salmon now apparent in some sections.

In this early era of Alaska's salmon fishery, prevailing attitudes about potential salmon predators were often based on anecdotal evidence, not scientific studies. Yet, these views were strongly held and vigorously defended. For example, it was then claimed that bears on Kodiak Island could eat one-third of their weight in salmon per day, an apparent horrendous loss of fish, especially since the bears wastefully littered the streams with partly devoured salmon carcasses. Bald eagles ripped into the flesh of adult salmon, gulls pecked out the eyes of spawning salmon and ate their eggs, and mergansers, charr, sculpins, and others gobbled up salmon eggs and young. Predator control programs seemed an obvious way to curtail these apparent losses and help protect the salmon runs for commercial harvest.

In 1915, E. Lester Jones, USBF Deputy Commissioner of Fisheries, reacted to these salmon losses by recommending a federal bounty on eagles and removal of existing protective laws on gulls and other waterfowl so their eggs could be legally harvested for human food. The Alaska Territorial Legislature enacted a bounty on eagles in 1917 and this law continued until 1953; well over 100,000 eagles were killed during this period in Alaska. Based on current ecological perspectives, many of these predator control efforts were misguided, ineffective, or counterproductive, but they were, nevertheless, strongly supported by the commercial salmon industry and by most governmental agencies and fishery biologists in the early 1900s. Jones (1915) aptly summarized a common belief about Alaska's salmon resources and the losses to salmon predators:

> [Speaking of Alaskan salmon, 1914] Of course, this great natural resource was made for man's use, and we must recognize, in every way possible, the fact that he has first claim and that the fish are there to be taken, but properly and with discretion, so that the future supply will not be jeopardized.

Throughout Karluk's early fisheries history, charr were stigmatized as destructive predators of the early life stages of sockeye salmon and were scorned by the salmon packing industry. As sockeye harvests declined over the

Dolly Varden, Karluk River weir, 1970. (Benson Drucker, Reston, VA)

years, charr predation on salmon eggs and juveniles received part of the blame. Most cannery officials and workers, fish culturists, biologists, and governmental officials of this era considered charr to be trash fish or vermin that should be destroyed whenever possible. Consequently, considerable effort, both official and unofficial, was devoted for many decades to reducing charr populations at Karluk, with the confident expectation that salmon runs would benefit. Early on, Turner (1886) and Bean (1891) mentioned that many Dolly Varden were harvested each year near Karluk Spit; these fish had some commercial value when packed in salt and shipped in barrels to markets in California. Yet, once canneries began to pack sockeye salmon, Dolly Varden incidentally caught in nets were discarded and left to die on the beach. Somewhat later, Jones (1915) argued that Dolly Varden had excellent food value and should be commercially harvested, not wasted.

The widespread concern about fish predators eventually led to a bounty system on charr in some parts of Alaska during 1920–41 (Hubbs, 1941). USBF employee Dennis Winn initiated a bounty system in 1920 at Bristol Bay, Alaska, where charr predation on juvenile sockeye seemed to be especially destructive. Payments varied from 2.5 to 5 cents per charr killed, with funds coming from the salmon canneries, Territory of Alaska, and U.S. Government. The federal Works Progress Administration funded the bounty program during the Great Depression of the 1930s as a way to boost the finances of local citizens. Though predator control seemed to be a straightforward way to benefit salmon numbers, in actual practice the effectiveness of the charr bounty was questionable. Carl Hubbs (1941) investigated federal management of Alaska's salmon fisheries in 1939 and focused attention on abuses in the bounty program. For example, he found that many fish tails redeemed for bounty payments were in fact juvenile salmon and other valuable salmonid species, not charr. His report, along with new scientific evidence on charr food habits, ended the charr bounty program in Alaska in 1941.

Apparently, bounties were never paid for destroying charr at Karluk during 1920–41, though several nearby canneries paid Henry Looff to kill these fish in streams entering Olga Bay on southwestern Kodiak Island.[1] According to Charles Turner, USBF warden and Karluk River weir tender during the 1930s, no bounties were paid for destroying Karluk's charr during that decade.[2] Likewise, Steele Culbertson, USBF warden for the Kodiak District, declared in his 1938 annual report "that Kodiak is not within the limits set forth in the Territory, wherein a bounty is paid for the destruction of predatory Dolly Varden trout."[3] Nevertheless, the USBF encouraged its Karluk employees and others to destroy Dolly Varden and other salmon predators whenever possible during 1920–41. Thus, Karluk's historical fisheries literature documents that charr, especially Dolly Varden, were regularly decimated for at least 60 years (1880–1941), though the actual number killed is unknown. Following, we discuss the methods and locations used to capture and destroy Karluk's charr during the predator control era.

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[1] 1) Rich Willis H. 1930 notebook (27 June). Location of original notebook unknown; copies at NARA, Anchorage, AK, and ABL Library, Auke Bay, AK.
2) Letters (1 July 1997 and 25 January 1998 [sent posthumously]) from Charles P. Turner, Kingston, WA, to Richard L. Bottorff, South Lake Tahoe, CA.

[2] See footnote 1 (2).

[3] Culbertson, J. Steele. 1938. Kodiak–Afognak District, 1938, Report of fishery operations. Department of Commerce, USBF. Unpubl. report. 44 p. Located at ABL Library Files, Auke Bay, AK.

Dolly Varden caught in a beach seine, Karluk Spit, 1954. (John Q. Hines, Mt. Shasta, CA)

Beach Seine Operations at Karluk Spit and Other Commercial Fishing Methods

Starting in 1882 and continuing for many decades, commercial fishermen used beach seines to harvest sockeye salmon in the river and ocean near Karluk Spit for the nearby canneries. Incidental to the salmon catch, each seine haul netted many hundreds and thousands of Dolly Varden. These fish had migrated down the Karluk River to the ocean in May–June and were feeding on marine fishes and crustaceans near Karluk Spit. Considering the large number of seine hauls made during a fishing season, the number of Dolly Varden captured and destroyed must have been large.

The first biologists to observe the Dolly Varden being caught in the commercial beach seines at Karluk Spit were Tarleton Bean in 1889 and Cloudsley Rutter in 1903, both employees of the U.S. Fish Commission. The early canneries attracted many scavenging fish, birds, and other animals to the area because of the fish wastes (eggs, viscera, and body parts) dumped into the lagoon and nearby ocean. It was believed that Dolly Varden accumulated around Karluk Spit to feed on this offal, a behavior that increased their chance of being caught by beach seines:

> [Karluk Spit, 1889] No diminution of the supply of this trout has been observed. There is great destruction of this fish at Karluk in the seining for Red Salmon, where thousands of Dolly Vardens are taken and left lying unused on the beach.
>
> [Karluk, 1903] The chief enemy in Alaskan fresh waters is the Dolly Varden trout, and from this pest Karluk Lake is practically free. At all salmon packing stations, the Dolly Varden, along with other fishes, collects in great numbers about the canneries to feed on the refuse. The cannery, therefore, is an important source of food supply for the enemy of the salmon on which the cannery depends for its existence. Thus the cannery tends to destroy itself. This is true as a rule, but Karluk is an exception. Here the salmon for the cannery are taken with seines in the immediate vicinity of the canneries so that large numbers of trout are taken and incidentally killed by being hauled out on the beach. There may be as many as 2,000 trout taken this way in one haul of the seine, and 500 is about the average number. Many of them get back into the water, as no particular care is taken to prevent their doing so, although a slight effort in that line would be well worth while. But even under the present conditions, there is no other station where the trout are so effectively destroyed, for at no other station is so large a proportion of the salmon taken so near the cannery and with seines. The consequence is that trout are practically unknown on the spawning beds of the salmon at Karluk Lake. During a four days' exploration of all the streams tributary to the lake where many thousand salmon were spawning, only 9 trout were seen . . . Such freedom from enemies as there is in Karluk Lake is absolutely unknown in any other locality. [4]

And yet, when Rutter actually examined the stomachs of Dolly Varden, none contained cannery refuse or young salmon. Nevertheless, he continued to believe that these fish ate many juvenile sockeye and recommended that they be captured during their spring migration down the Karluk River.

Few observations exist in Karluk's fisheries literature of the number of Dolly Varden destroyed by

[4] Rutter, Cloudsley Louis. 1903. Field observations by Cloudsley Rutter on his Karluk work of 1903. Unpubl. notes. 48 p. Copy provided by Mark R. Jennings (Davis, CA) and located in Box 130, Barton Warren Evermann papers, Library Special Collections, California Academy of Sciences, San Francisco, CA.

beach seines between 1903 and 1921 because few biologists then visited Karluk for extended periods and those that did focused their attention on the hatchery operations at Karluk Lagoon. But once the counting weir began operating on the lower Karluk River in 1921, the seasonal migrations and abundance of Dolly Varden were closely observed each year, as were the nearby beach seining operations at Karluk Spit. Research biologists and weir tenders often witnessed Dolly Varden incidentally caught in beach seines and firmly believed that destroying these fishes enhanced salmon survival:

> [Karluk River weir, early August 1925] Trout were not very plentiful large numbers being caught by commercial fishermen outside.
>
> [Karluk River weir, 1–15 July 1931] During the second week of July quite a few trout started to go up the river and a good many were caught at the Spit in the salmon seines.[5]

John Hines, FWS stream guard in 1954 and 1956, found that it was standard practice for fishing crews to pull the seine onto Karluk Spit, take the salmon, and leave all other fishes on the beach.[6]

Though beach seining annually destroyed many Dolly Varden at Karluk Spit, little information exists of the incidental catches made by other fishing methods, except for that mentioned by Morton (1982) during 1937–41:

> [Karluk, 1937–1941] Thousands of Dolly Varden charrs were killed annually by the four types of salmon-fishing gear employed by the commercial fishery from Cape Karluk to Uyak Bay. Two of these types were of a mobile nature: 1) the purse-seine fishing vessels, and 2) the Alaska Packers Association 300-fathom-long, power-operated beach seines which fished near the mouth of the Karluk River. The other two types were of an immobile or stationary nature: 1) the local gill-netters who occupied the same sites year after year from Cape Uyak to Parks Cannery in Uyak Bay, and 2) the huge, pile-driven traps that extended out from shore.

He claimed that the commercial ocean traps caught thousands of Dolly Varden (7,538 in 1937 and at least 1,625 in 1938–39), while purse seines and gill nets took unknown additional numbers. During these years, the salmon canneries converted Dolly Varden and other undesirable fishes into fish meal.

In summary, it is difficult to know the true impact of commercial fishing on Dolly Varden abundance at Karluk because almost no data exists on the total catches and natural populations of these charr. Without a doubt, the commercial fishery annually removed large numbers of Dolly Varden and these actions continued for many years.

Operation of Karluk Lagoon Hatchery, 1896–1916

The APA operated a sockeye salmon hatchery on Karluk Lagoon in 1896–1916, and during those 21 years they took 628,107,000 sockeye eggs and released 488,754,000 fry back into the river's estuary. They hoped that released fry would bolster Karluk's sockeye salmon runs. Of course, hatchery superintendents wanted to maximize survival of newly released fry and were concerned that predators may concentrate near release sites and decimate the small fish. To reduce predation losses, fry were transported to lagoon sites that had protective vegetative cover or rocky substrates and away from inflowing streams where fish predators lurked. Prior to fry release, hatchery workers often seined the lagoon to remove Dolly Varden, though the actual number killed remains unknown:

> [Karluk Lagoon, spring, 1909–1910] We went down the river and seined thousands and thousands of Dolly Varden, dragging them up on the bank to die. Every one of them was there to gorge on salmon fry and would have eaten fifty or more a day. Once the Dolly Varden population was reduced, we turned loose the young salmon and after that they were on their own. (Taylor 1964)
>
> [Karluk Lagoon hatchery, 1911] This live car is an old skiff with wire mesh-covered ports in the sides and is towed to grounds near the hatchery, where there is a good growth of eelgrass. The ports are then opened and the fry swim out at their leisure. Trout and sculpins no doubt devour quite a number of the young salmon. Last season large numbers of trout were seined near the pond outlet. (Bower 1912)

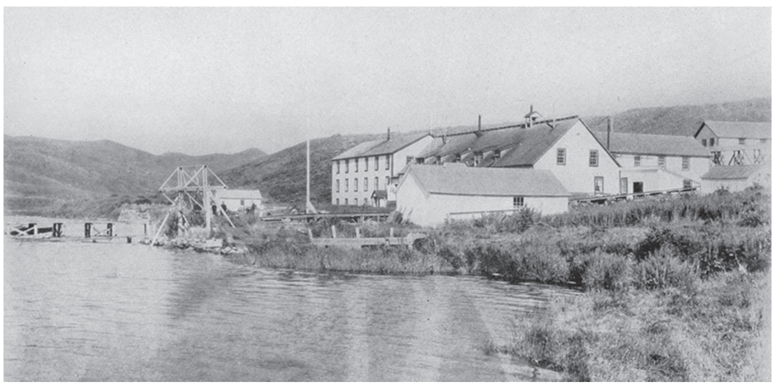
Karluk River Weir, 1921–42

Because Dolly Varden annually migrated between Karluk Lake and the ocean, these fish were easily concentrated and destroyed at the Karluk River weir during 1921–42. Each spring during their down-migration, Dolly Varden accumulated above the weir and large numbers were captured and killed with traps, seines,

[5] 1) Hungerford, Howard H. 1926. Report of operations at Karluk weir for season of 1925. Department of Commerce, USBF. Unpubl. report. 3 p. Located at NARA, Anchorage, AK.
2) Wood, Ray S. 1931. Report of the Karluk River weir, 1931. Department of Commerce, USBF, Karluk, AK (Attached to report of Hungerford 1931). Ten unpubl. reports. Located at ABL Library Files, Auke Bay, AK.

[6] John Q. Hines, Mount Shasta, CA, personal commun. with Richard L. Bottorff, 1998.

Alaska Packers Association hatchery on Karluk Lagoon, 1897. (Frederic M. Chamberlain or Harry C. Fassett, from Moser, 1899)



Alaska Packers Association hatchery on Karluk Lagoon, 1914. (W. H. Burnet, from Jones, 1915)

Dolly Varden caught in a seine haul, Karluk River, 1914. (W. H. Burnet, from Jones, 1915)

web pots, gill nets, hook-and-line, and dynamite. During their up-migration in July–August, weir devices caught additional Dolly Varden. Although records are incomplete, typically 5,000 to over 80,000 Dolly Varden were annually destroyed at the weir in this 22-year period (Table 9-1). The USBF encouraged weir tenders to capture Dolly Varden and provided funds for supplies, but workers received no bounties or extra payments for this chore. Predator control work was then considered a spare time duty. Upon hearing of these control efforts in 1922, an APA official wrote to U.S. Commissioner of Fisheries Henry O'Malley: "I am glad to hear that you

Table 9-1
Dolly Varden destroyed at Karluk River weir, 1921–42.

Year	Number killed	Comment
1921		
1922	18,635	Web pots and dynamite used at weir.
1923		Traps used at weir.
1924		
1925	30,221	Traps used at weir.
1926	5,609	Number of Dolly Varden killed to 30 May. Traps used at weir.
1927	26,122	Seines, traps, and gill nets used at weir. Charr killed at Karluk Lake?
1928	29,000	
1929	10,800	Possibly 50,000 charr killed at Karluk Lake in 1929 or 1930.
1930	13,500	Possibly 50,000 charr killed at Karluk Lake in 1929 or 1930.
1931	8,000	Many Dolly Varden captured in beach seines at Karluk Spit.
1932	14,688	Considerable number of Dolly Varden destroyed.
1933		Seine and traps used at weir.
1934		
1935		Traps used at weir.
1936		
1937	81,539	Traps used at weir.
1938	51,385	Traps used at weir.
1939	51,500	Traps used at weir.
1940		Traps used at weir.
1941		No traps used at weir. No bounty for Dolly Varden.
1942		Traps may have been used at weir.
TOTAL	340,999	Minimum number destroyed at weir during 1921–42.

are destroying Dolly Varden trout migrating into the Karluk River."[7]

Dolly Varden destruction at Karluk during this era was part of a larger predator-control program by the USBF to enhance salmon numbers. Besides Dolly Varden, the control effort included destruction of predatory and scavenging birds (bald eagles, gulls, kittiwakes, terns, loons, and mergansers). Weir tenders searched for and destroyed merganser nests along the Karluk River and shot bald eagles whenever possible.[8] To gather actual evidence of the predation, these employees were instructed in the 1920s to collect the stomachs of fish-eating birds for analysis by the U.S. Bureau of Biological Survey.[9]

The most dramatic way to destroy Dolly Varden at the weir was with dynamite, though it could only be used for a brief period in early spring before the sockeye smolts arrived on their downstream migration:

> [Karluk River weir, 22–23 May 1922] Five sticks of dynamite secured from the Alaska Packers were set off by electricity in an eddy where the trout gather about 50 yards above the rack. It killed 48 dollies, 3 steelheads and no small fish that we could see . . . Most of the day was put in seining and dynamiting trout. 254 were killed with four shots of powder of 1 stick each.
>
> [Karluk River weir, 9 June 1922] Received wire granting $100 more for dolly destruction but unable to use it as the water to high and the trout are leaving.
>
> [Karluk River weir, 1922] Dynamite exploded at any desired moment by means of an electric battery was tried also in killing the Dolly Varden trout with good success. The trouble with this method is that there were only a few days after the trout began to gather above the weir before schools of young red salmon began to come downstream when the practice had to be stopped.[10]

An attempt was made in 1927 to capture down-migrating Dolly Varden with gill nets, but these fish, after a long winter at Karluk Lake, were so thin that

[7] Letter (27 June 1922) from William Timson, APA, San Francisco, CA, to Henry O'Malley, U.S. Fish Commissioner, Washington, DC. Located at NARA, Anchorage, AK.

[8] 1) Letter (25 November 1921) from Fred R. Lucas, Fish Culturist, Parkplace, OR, to Henry O'Malley, Field Assistant, Seattle, WA. Located at NARA, Anchorage, AK.
2) Rich, Willis H. 1922–1931 notebooks. Location of original notebooks unknown (in 1956, Rich had the original notebooks); copies at NARA, Anchorage, AK, and ABL Library, Auke Bay, AK. In 1963 the BCF, ABL published the notebooks as a Manuscript Report.

[9] Lucas, Fred R., Ray S. Wood, Forsyth and G. O. Thompson. 1922–1923. Daily notebook of operations at the Karluk weir in 1922 (22 April–November) and 1923 (May–October). Located at NARA, Anchorage, AK. The results of the bird stomach collections (May–June 1922) are unknown.

[10] 1) See footnote 9.
2) Lucas, Fred R. 1924. Summary of red salmon census for the season of 1922 at Karluk Alaska. Department of Commerce, USBF. Unpubl. report. 5 p. Located at NARA, Anchorage, AK.

their gill plates failed to catch in the net. Seines were used above the weir to capture Dolly Varden in the spring of 1928, and USBF biologist Seymour Smith noted that "the dead fish finally sluiced along an improvised aqueduct running through an opening in the pickets."[11] Seining was an ineffective method for capturing Dolly Varden when sockeye smolts were present in the Karluk River.

Both downstream and upstream weir traps eventually became the preferred method to capture migrating Dolly Varden. Once installed, traps continuously caught fish, but often so many accumulated that it became a major chore to empty the traps:

> [Karluk River weir, 1922] The actual count of Dolly Varden trout killed is 18,635. We could not see that this number made the least difference in the amount hanging around above the weir the last of May and first of June. . . . The trout entered the trap fine but the labor of lifting and replacing the trap in the swift water and pewing and counting the trout was quite a task for two men and would take about as long as it did to get the fish in the trap in the first place. . . . It is my opinion that at least 50,000 dollies were in sight above the rack at one time and with adequate means of handling a trap or possibly two traps we could have taken about all of them.
>
> A web pot 16 by 16 feet with V throat was purchased in Seattle to try and catch some of the Dolly Varden trout coming down stream in the spring. After considerable difficulty owing to the swift water we succeeded in hanging it below a gate at the lower end of the rack on May 20th and that afternoon caught 338 trout of an average length of about 12 inches [305 mm]. High water made setting the trap impossible again until the 22nd and then the number of trout increased daily until June 3 when we caught 4003. The trap was lifted twice that day and the last time was fishing only two hours and caught 1500 Dolly Varden trout and a great many steelheads.
>
> The two of us could not lift the entire trap-load of fish out bodily and had to dip them which required more time than the catching and no more men could be secured at that time but if we could have had a crew of about six men to handle and repair the trap and keep the steelheads dipped out, a great deal many more trout could have been caught. . . . All of these trout above the weir were in poor flesh and upon examination had nothing or the most very little in their stomachs and the eggs in the egg roe of the females were about the size of a pinhead. . . . A beach seine is not practical for catching trout above the weir on account of the swift water and the necessity of always getting wet even with waders on at this time of the year.[12]

Dolly Varden captured at the Karluk River weir near Karluk Lagoon, May 1939. (William M. Morton, from Robert S. Morton, Portland, OR)

Morton (1975) described the daily routine of maintaining and emptying the Dolly Varden trap in 1939:

> Each morning we brailed the "trout" from the live trap into a skiff, allowed them to die, then took weights and measurements, particularly of all tagged or marked specimens and then tossed them over the weir. By the end of May, the main channel of the river bottom was white with their carcasses for a mile and a half below the weir.

Despite two decades of predator control work, doubts arose in 1940–41 about the value of removing Dolly Varden to benefit Karluk's sockeye salmon. Surprisingly, the available food habits studies showed that few Dolly Varden actually ate juvenile sockeye, and it was argued that destroying Dolly Varden might be counterproductive if they preyed heavily on sticklebacks and sculpins, these two fishes being competitors or predators of juvenile sockeye (DeLacy, 1941; Morton,

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[11] Smith, Seymour P. 1928 notebook. Original notebook location unknown; copy located at NARA, Anchorage, AK.

[12] 1) Letter (11 June 1922) from Fred R. Lucas, USBF, Uyak, AK, to Field Superintendent, USBF, Seattle, WA. 2) Lucas, Fred R. 1924. Summary of red salmon census for the season of 1922 at Karluk Alaska. Department of Commerce, USBF. Unpubl. report. 5 p. Both located at NARA, Anchorage, AK.

1982). Morton and DeLacy claimed "these findings indicate that a large scale program of char removal on the Karluk River might well lead to a decline rather than to an increase in the red salmon populations."[13] Thus, Ralph Ferrandini, FWS fishery management agent, stated in his Kodiak District report for 1941 that Dolly Varden traps were not used, the benefits of destroying these fish being controversial.[14] The Dolly Varden bounty program ended throughout Alaska in 1941, but two weirs on Kodiak Island reportedly used traps in 1942 (Bower, 1944). It appears unlikely that Karluk was one of these trap sites since the weir operated at its new Portage location in 1942.

Steelhead Weir at Karluk River Portage, 1927–32

Each spring during 1927–32, the USBF installed a temporary weir at Karluk River Portage to intercept down-migrating adult steelhead and take several million eggs for hatchery incubation. As steelhead accumulated above the weir, workers caught them in seines, along with many Dolly Varden migrants. Little information exists about the fate of captured Dolly Varden, but apparently they were destroyed:

> [Karluk River Portage, spring 1927] A picket weir . . . across Karluk river is located here . . . for use in taking approximately 5,000,000 steel head eggs which were shipped to the States; it is also used in killing off Dolly Varden trout. Have been advised that this work will be continued indefinitely. [15]

USBF biologists Harry Baer and H. Olafson helped take steelhead eggs in May 1932 before assuming their weir-tending duties. They claimed that 7,800 Dolly Varden were destroyed at the Portage weir that year.[16] Thus, during 1927–32, workers regularly removed Dolly Varden at the steelhead weir, as well as at the salmon counting weir downstream. The FWS, ADFG, and Kodiak Conservation Club, with the assistance of the U.S. Navy, again took steelhead eggs at the Karluk River Portage during 1953–59, but incidentally captured fish were released alive back to the river below the weir.

Seining Operations at Karluk Lake

Nearly all charr control efforts at Karluk in 1882–1941 focused on Dolly Varden, as these fishes were easily captured and destroyed during their annual migrations up and down the river. All of this work had little effect on the non-migratory Arctic charr population that resided in Karluk Lake, even though those fish were also suspected of preying on sockeye eggs and juveniles. Apparently a few attempts were made to remove Arctic charr from the lake, but these never were sustained efforts that lasted more than a year or two. The USBF proposed in their 1927 research plans to reduce charr numbers at Karluk Lake, but it is unclear if this work was actually done:

> [Proposed 1927 research program at Karluk] To carry on intensive fishing operations for predatory fishes at counting weir, in river above weir and in the tributary streams of Karluk lake . . . The usual crew of three men employed on the weir who in their spare time can destroy predatory fish.[17]

Years later, several biologists mentioned these past efforts to control the charr at Karluk Lake, but few details exist except that the USBF and Territory of Alaska spent $4,000 to remove thousands of charr over two years:

> [Concerning past efforts to control charr at Karluk Lake] Talked to Hoffstad—tell of going to lake in '28 & '29 taking 32 & 40,000 trout out of lake by $4,000 grant from territory of Alaska—he believes in them as killers alrite.
>
> . . . the efforts of the Territory of Alaska to seine out the "dollies" from the lake in 1929 and 30 or thereabouts. This undoubtedly proved more harmful than beneficial to the salmon, our recent studies of the lake charrs indicates . . . I still maintain that Hoffstad's removal of large numbers of charrs (50,000 per season he told me) mostly of the lake type no doubt, in 1929 or 30 or thereabouts was probably followed by abnormally successful broods of sticklebacks . . .
>
> For many years, during which the Karluk red salmon runs continued to decline, the anadromous charrs in the Karluk River as elsewhere in Alaska were persecuted vigorously (through use of the bounty system). Also, during this period seining operations were carried on at Karluk Lake on one or two occasions,

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[13] FWS. 1941. North Pacific and Alaska Biological Fishery Investigations, Annual Report for 1941. Located at NARA, Anchorage, AK.

[14] Ferrandini, Ralph A. 1941. Kodiak–Afognak Report, 1941, Alaska fishery operations. U.S. Department of Commerce, USBF. Unpubl. report. 41 p. Located at ABL Library Files, Auke Bay, AK.

[15] Letter (15 September 1927) from Fred J. Spach, Junior Engineer, Alaska Road Commission, Juneau, AK, to M. C. Edmunds, Superintendent, Alaska Road Commission, Anchorage, AK. Located at NARA, Anchorage, AK.

[16] Baer, Harry D., and H. Olafson. 1932 notebook. Located at NARA, Anchorage, AK.

[17] Letter (3 December 1926) from Howard H. Hungerford, Warden, Alaska Service, USBF, Seattle, WA, to Dennis Winn, Agent, USBF, Seattle, WA. Located at NARA, Anchorage, AK.

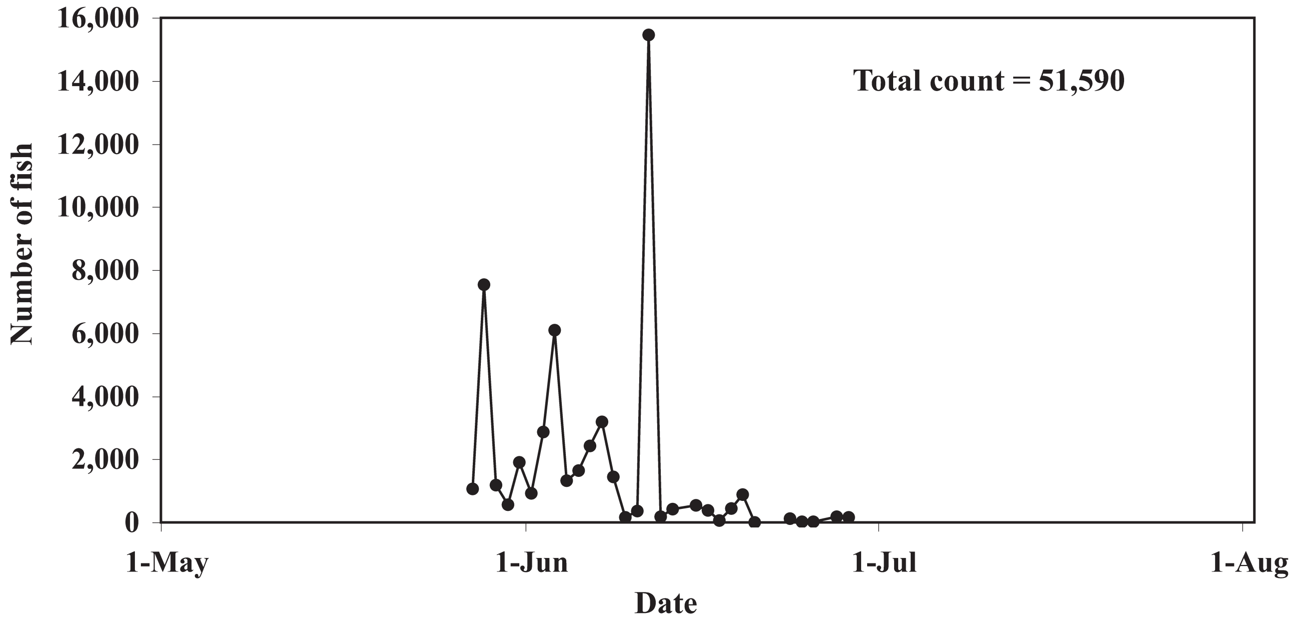


Figure 9-1. Number of down-migrating Dolly Varden counted through the Karluk River weir, 1956. The weir was installed near the lake's outlet on 20 May 1956. Unpublished BCF data from NARA, Anchorage, AK.

> unrecorded numbers of each species of charrs were destroyed. It appears probable that the numbers of each were reduced.
>
> Years ago a rather comprehensive seining and trapping program of Dolly Varden and Charr was undertaken at Karluk. Unfortunately no measure was made of the reduction in the Charr and Dolly Varden population.[18]

Summary of charr control efforts

Because of the persistent predator control efforts at ocean beach seine sites, the river weirs, and the sockeye hatchery, Dolly Varden sustained huge losses in the Karluk system during 1882–1942, while sporadic attempts to control Arctic charr in the lake probably had little effect on their population. Though the true numbers of Dolly Varden destroyed during this period remain unknown, the methods for capturing them were very effective and potentially a significant part of the population was eliminated each year. Yet, even with these losses, large numbers of migrating Dolly Varden continued to accumulate at the weir year after year, suggesting that they remained abundant and that the control methods were only partially successful. Since no past or present population estimates exist for Karluk's Dolly Varden, it is difficult to interpret the impact of these past control efforts.

An estimate of the Dolly Varden population could be obtained by counting them as they migrated past the Karluk River weir. Reportedly such counts were made in some years, but these data remain unpublished. When down-migrating Dolly Varden were counted at the weir in May–June 1956, they totaled at least 51,590 (Fig. 9-1), with an unknown number of additional fish having migrated downstream before the weir was installed on 20 May. If the magnitude of the 1956 migration was typical, a substantial proportion of the Dolly Varden population was destroyed each year during 1921–42. Anecdotal evidence does exist that Dolly Varden populations were smaller immediately after predator controls ended in 1941 or 1942. For example, Shuman explored Karluk Lake in 1943 and reported seeing few charr:

> [Speaking of Karluk Lake charr, 1940s] There is little information on the abundance of resident lake fishes (other than red salmon) either now or in past decades, but there is considerable reason to believe that the abundance of lake charrs has decreased sharply, and that the abundance of sticklebacks has increased many fold. Early investigators all remarked upon the high

[18] 1) Morton, William M. 1940 notebook (2 September). Original notebook in personal papers of Robert S. Morton, Portland, OR.
2) Morton, Mark. ca. 1942. No title. Unpubl. report. 3 p. Located at NARA, Anchorage, AK.
3) Shuman, Richard F. 1951. Trends in abundance of Karluk River red salmon with a discussion of ecological factors. Manuscript prepared for Fish. Bull. 71(52). Unpubl. report. 56 p. Located at ABL Office Files, Auke Bay, AK.
4) Letter (11 June 1957) from [Phil Nelson ?], FWS, Annapolis, MD to John Owen, FWS, c/o Roy Lindsley, Kodiak, AK. Located at NARA, Anchorage, AK.

abundance of Dolly Varden and Arctic charr, both in the lake and in the tributary streams . . . On the other hand, although I spent considerable time at the lake in 1943 and during subsequent seasons, it was not until 1946 that I saw Dolly Varden or Arctic charrs in any of the affluents, and even within the lake itself I saw, or took by rod and line, only a few. . . .[19]

Historical Evidence of Charr Food Habits and Predation on Sockeye Salmon

Throughout most of Karluk's fisheries research history, the true status of charr as serious or inconsequential predators of sockeye juveniles and eggs has been a particularly puzzling topic. The overwhelming consensus between 1882 and 1941 declared that charr should be destroyed because they consumed many sockeye young and eggs. This conclusion, an accepted belief throughout Alaska and the Pacific Northwest, was not based on direct evidence from Karluk. In stark contrast, when biologists actually studied charr predation on Karluk's young sockeye in 1939–41, it appeared to be negligible. Since these two views of charr predation differed so completely, field biologists at Karluk after 1941 questioned both conclusions and personally examined at least some charr stomachs to learn the real truth. That is, prior to 1941 biologists examined charr foods to see if predation was really as bad as reported; after 1941 they examined foods to see if predation was really as good as reported. This sense of disbelief about both viewpoints continued into present times, when the idea developed that charr predation on Karluk's juvenile sockeye is minimal at most times and places, but is substantial at specific times and places.

In this section, we examine historical evidence of charr predation on Karluk's sockeye juveniles and eggs, including charr food studies and the charr-sockeye relationship.

Early Records of Charr Food Habits (1889–1920)

The first biologists and officials that visited Karluk believed that charr preyed seriously on sockeye young and eggs. When Bean (1891) reconnoitered Karluk Lake in 1889, charr were common and he claimed they consumed "large quantities of the fresh salmon eggs" and fry. He observed Dolly Varden eating sockeye eggs discarded from the canneries at Karluk Spit. George Tingle (1897), Inspector of Salmon Fisheries, and Jefferson Moser (1899), Commander of the U.S. Fish Commission steamer *Albatross,* stated the prevailing beliefs about charr:

[Karluk hatchery, 1896] If it were not for the salmon trout, which is the wolf of the family, there would be no necessity for these hatcheries; but, strange to say, this villainous trout, which gathers in numbers under the female salmon as she is spawning on the nest and eats the eggs as fast as they appear...

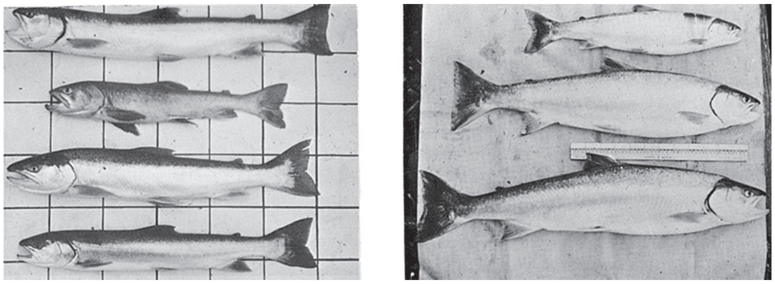
[Speaking of Alaska, 1897] Early in the spring, or shortly before the redfish commence to run, the Dolly Varden comes to the mouth of a stream and awaits the salmon . . . [and] follow the salmon to the spawning-beds. On the spawning-grounds, when the ripe fish deposit their eggs, the trout consume them in immense numbers. The Dolly Varden has been seen to take the salmon eggs as they were dropped. The salmon know these egg destroyers and will frequently dart at the trout, but the latter are quicker in their movements and get away without injury.

While inspecting the Karluk Lagoon hatchery in 1900, Fassett (1902) found a 64 mm Dolly Varden in a nursery pond with 12 sockeye fry in its stomach and recommended that fry only be released into the lagoon in winter since Dolly Varden fed less in that season.

Rutter examined the food habits of Karluk's charr in 1903 to learn if they preyed on juvenile salmon, but typical of initial attempts at answering biological questions, his study was unclear. He installed a trap at the lake's outlet and caught 190 charr between 5 June and 25 July (Chamberlain, 1907). To his surprise, most charr had empty stomachs and none had young salmon, even though salmon juveniles swam nearby. Those charr with food had eaten sculpins, aquatic insects, other invertebrates, and salmon eggs. Of 131 charr he collected from a salmon spawning stream in August, most had fed on salmon eggs and maggots that infested the numerous salmon carcasses. Several hundred Dolly Varden incidentally caught in ocean beach seines at Karluk Spit in late July had eaten crustaceans, sand lances, and young codfish. Only Dolly Varden collected from the unnatural hatchery corrals at Karluk Lagoon had eaten a few sockeye salmon fry in July. Thus, Rutter found little evidence of charr predation on juvenile sockeye, though charr obviously ate many salmon eggs:

[Speaking of Karluk's Dolly Varden, 1903] Much complaint is made that this fish destroys great numbers of young salmon, and the complaint is doubtless well founded, though above data do not so indicate. It would pay to set traps on the river before the salmon run, in order to catch the trout, for it is the early trout that catch the most young salmon. After the canneries

[19] See footnote 18 (3).



Down-migrating (left) and ocean-caught (right) Dolly Varden, Karluk River. Note the poor condition of the down-migrants and excellent condition of the fish after they spent some time at sea. Second fish below top of left photograph is an Arctic charr. (William M. Morton, from Robert S. Morton, Portland, OR)

> begin work, they may be seen feeding at any high tide, though none of the sea examples contained such offal. At that time there are abundant young sand launces and cod so they do not need to prey on the young salmon so much.[20]

Rutter seemed unconvinced by his food studies and continued to declare that charr were serious salmon enemies that destroyed many young salmon each spring in Karluk Lagoon. Why he believed this is unclear, though possibly his previous experiences of 1896–97 while working at Karluk's hatchery influenced his ideas. Dolly Varden then preyed on the numerous hatchery fry released into the estuary. And yet, Rutter also believed Karluk Lake to be nearly free of charr because commercial beach seines incidentally captured and destroyed many of these fishes. During a four-day exploration of the lake's spawning streams in 1903, he saw thousands of sockeye salmon, but only nine charr, a scarcity unknown in Alaska. Notwithstanding Rutter's inability to document substantial charr predation at Karluk, Jordan and Evermann (1904) declared in their report of the Alaska Salmon Commission that "this trout is the most persistent and destructive enemy of the salmon eggs and fry. They follow the salmon to their spawning beds, where they devour the salmon eggs and fry by the millions." In any event, Rutter was the first Karluk biologist to test the established dogma about charr predation by checking their food habits. Significantly, his field studies indicated that charr predation may be less serious than commonly alleged.

Dolly Varden predation was a persistent concern at the Karluk Lagoon hatchery in 1896–1916. Hatchery superintendent James Richardson wanted to move the hatchery upstream to Karluk Lake in 1904 to give released fry time "to grow in size and strength before reaching the haunts, lower down the stream, of their terrible enemy, the salmon trout" (Kutchin, 1905). Dolly Varden were thought to consume as many as 50 sockeye fry daily from hatchery releases in 1909 (Taylor, 1964). To minimize losses, hatchery workers released fry into areas of protective cover (Roppel, 1982) or after Dolly Varden were removed. Fassett in 1910 discounted the intensity of predation on hatchery-released fry, claiming that it only lasted a few days:

> [Speaking of newly released sockeye salmon fry at Karluk Lagoon, 1910] Trout seem to prey upon the fry for but a very short time, according to the superintendent's observations. He says that for two or three days the trout will be noticed in pursuit of the young salmon but after that they seem to mix together and cruise around the lagoon in company.[21]

Dolly Varden Food Habits at the Karluk River Weir (1921–38)

Once the Karluk River weir began operating in 1921, biologists observed the annual Dolly Varden migrations and occasionally examined a few fish to see if they had preyed on juvenile sockeye, especially on the abundant smolts:

> [Karluk River weir, 1921] There was a surprisingly large down stream movement of spent Dolly Varden Trout . . . From May 28th to June 10th, thousands of Dollies were gathered above the rack. . . . These Dollies were in very poor physical condition and kept getting thinner while observed in the vicinity of the rack. On June 9th and twice later I examined the stomachs of several spent Dollies and found no evidence of recent feeding.
>
> [Karluk River weir, spring 1921] I examined the stomachs of nearly fifty of the dollies at different times during the migration of the young salmon and in none of them found any indications of recent feeding.
>
> [Karluk River weir, 21–23 May 1922] The lot of trout caught yesterday would average 1 ft. [305 mm] long and one specimen measured 26 ¼" [667 mm]. I examined 29 of these fish . . . and found no evidence of recent feeding . . . The dollies examined have not been feeding lately.

[20] See footnote 4.

[21] Fassett, H. C. 1910. Report on the salmon hatchery operated by the Alaska Packers Association on Karluk Lagoon, Kadiak Island, Alaska. Unpubl. report. 25 p. Located at Alaska Historical Collections, Alaska State Library, Juneau, AK.

[Karluk River weir, 2 June 1926] Today took scales and data from 105 dollies. These were of the lot which are going down stream. Stomachs of all were completely empty.

[Karluk River weir, 16 June 1926] In the seining in the Lagoon we caught a number of dollies which were apparently fresh in from the ocean—at least they were not like the lot taken at the weir on their way down. Were much brighter and cleaner and one opened had a number of small fish in its stomach. Couldn't identify the remains but from their size and general appearance they must have been small salmon 3" or 4" in [76–102 mm] length.

[Karluk Lagoon, 11 May 1935] lots of dollys in lagoon feeding on Hump fry which is abundant.[22]

Surprisingly, little evidence could be found that down-migrating Dolly Varden preyed on sockeye smolts in the lower river; most of these emaciated charr had empty stomachs. Similarly, up-migrating Dolly Varden also had empty stomachs, but these fish were in much better condition after feeding in the ocean and estuary for several weeks.

Charr Food Habits at Karluk Lake and its Tributaries (1921–38)

Biologists, fishery managers, and cannery officials seldom visited Karluk Lake prior to 1921, their main interests then being the cannery and hatchery operations near the river's mouth. The lake's remote location, rustic living conditions, and few supplies limited any visits to no more than a few days. But once the weir proved its value as a research and management tool in 1921, the focus of sockeye salmon research shifted upstream to better understand the biological conditions at Karluk Lake, including charr predation.

Though comprehensive studies of charr food habits were not done at Karluk Lake during 1921–38, several biologists gathered general information and examined a few charr stomachs (Tables 9-2, 9-3). Gilbert noted large Dolly Varden in the Upper Thumb River on 11 August 1921 and these fish were close to spawning as shown by their mature gonads and redd-building behavior. One 380 mm Dolly Varden had an empty stomach.

Rich (1963) spent much time at Karluk Lake during 1926–30 and occasionally saw charr in the lake and its tributary streams. At Meadow, Halfway, and Grassy Point creeks in August 1926, he watched Dolly Varden eat loose sockeye eggs but felt this did little harm because many of these eggs were dead, or, if alive, their survival was unlikely when not buried in the stream's gravel. The charr he caught on hook-and-line at Camp Island in July–August 1927 (probably Arctic charr) had eaten sticklebacks, stickleback eggs, aquatic insects, snails, and algae. One charr contained about 2,000 stickleback eggs (28 July 1927) and a 460 mm charr had eaten at least 12 adult sticklebacks (9 July 1930).

Seymour Smith, Rich's assistant, visited Karluk Lake in early spring 1927 to observe the migration of newly emerged sockeye fry from the tributary creeks into the lake. Ice still covered the lake when he arrived on 29 April and this limited his observations to Moraine Creek. A few fry still emerged from the creek's substrate, but most fry had already migrated to the lake. At the mouth of Moraine Creek he saw large aggregations of charr, these fish apparently preying on migrating fry. Revisiting the same site on 20 May, the charr concentrations were absent:

[Moraine Creek mouth, 29 April 1927] At the mouth of Moraine Creek and for a radius of approximately fifteen yards [14 m] was a school of dollies . . . It seems fairly obvious that these fish are waiting for the fry to drop down into the lake, from the spawning beds. It is also a question what the mortality of the fry emerging from the gravel of lake spawning beds might be, due to presence of these trout. [20 May 1927] It is a noteworthy fact that there are no more trout off the mouth of this creek, indicating that there are no more fry dropping to the lake....[23]

Later in 1927 Smith observed charr and juvenile coho salmon feeding on sockeye salmon eggs in Lower Thumb River.

Barnaby visited Karluk Lake in eight field seasons (1930–37) and regularly examined charr stomachs to determine their diet. In 1935 he began a detailed study of charr food habits and migrations to learn how these fish affected sockeye salmon. He soon realized that two charr types inhabited the Karluk ecosystem, one being migratory and another being lake residents. He called these two types the "sea-run population" and

[22] 1) Lucas, Fred R. 1922. Report of the census of red salmon that escaped to the Karluk Lake spawning grounds during the season of 1921. Department of Commerce, USBF. Unpubl. report. 14 p.
2) Letter (25 November 1921) from Fred R. Lucas, Fish Culturist, Parkplace, OR, to Henry O'Malley, Field Assistant, Seattle, WA.
3) Lucas, Fred R., Ray S. Wood, Forsyth, and G. O. Thompson. 1922–1923 notebook (21 May 1922).
4) Rich, Willis H. 1926–1931 notebooks (2 and 16 June 1926, 6 June 1930).
5) Hungerford, Howard H. 1935 notebook (11 May). All located at NARA, Anchorage, AK.

[23] Smith, Seymour P. 1927 notebook . Located at NARA, Anchorage, AK.

Table 9-2

Historic records of charr food habits at Karluk Lake and tributaries, 1921–70.

Date	Location	Charr[1]	Number sampled	Stomach contents[2]	Reference[3]
11 Aug. 1921	U. Thumb River	DV	1	empty	Gilbert, 1921, notebook
8 Aug. 1926	Meadow Creek	charr	few	salmon eggs	Rich, 1963
23 Aug. 1926	Grassy Point Creek	charr	many	salmon eggs	Rich, 1963
26 July 1927	Halfway Creek	charr	1	aquatic insects	Rich, 1963
28 July 1927	Camp Island	charr	4	SB young and eggs	Rich, 1963
3 Aug. 1927	Camp Island	charr	7	aquatic insects, SB young and eggs, snails	Rich, 1963
4 Aug. 1927	Camp Island	charr	7	SB eggs, aquatic insects	Rich, 1963
27 Aug. 1927	Thumb beach	charr	some	salmon eggs	Smith, 1927, field notes
9 July 1930	Camp Island	charr	3	SB and SB eggs	Rich, 1963
12 July 1930	Camp Island	charr	5	SB and SB eggs	Rich, 1963
12 July 1930	Karluk Lake	charr	some	SB and SB eggs	Barnaby, 1930, notebook
13 July 1930	Thumb Lake	charr	1	salmon eggs	Barnaby, 1930, notebook
16 July 1930	Little Lagoon Creek	charr	4	SB and SB eggs	Barnaby, 1930, notebook
13 May 1931	Camp Point	charr	some	aquatic insects	Barnaby, 1931, notebook
15 May 1931	Camp Point	charr	few	aquatic insects	Barnaby, 1931, notebook
23 Sep 1931	E. Fork Thumb River	DV	12	most empty, salmon eggs	Barnaby, 1931, notebook
22 July 1933	Grassy Point Creek	charr	2	salmon eggs	Barnaby, 1933, notebook
22 May 1934	S. Karluk Lake	charr	some	aquatic insects, sockeye fry	Barnaby, 1934, notebook
18 July 1935	Camp Island	charr	few	SB eggs, snails, clams	Barnaby, 1935, notebook
19 July 1935	Camp Island	charr	41	SB and SB eggs, snails, clams, algae salmon eggs, aquatic insects	Baranby, 1935, notebook
20 Jul 1935	Karluk Lake	charr	2	empty	Barnaby, 1935, notebook
21 Jun 1936	Island Point	charr	2	SB eggs	Barnaby, 1936, notebook
28 Aug 1937	Bear Point	charr	19	SB, salmon eggs, snails, aquatic insects	Barnaby, 1937, notebook
1939–1941	Karluk Lake	DV	many	aquatic insects, salmon eggs, snails leeches, sculpins, salmon flesh	DeLacy, 1941 Morton, 1982
1939–1941	Karluk Lake	AC	many	aquatic insects, salmon eggs and flesh SB and SB eggs, sculpins	DeLacy, 1941 Morton, 1982
11 July 1943	Eagle Creek	DV	2	salmon eggs	Shuman, 1943, notebook
11 July 1943	Eagle Creek	AC	8	most empty, aquatic insects	Shuman, 1943, notebook
13 July 1943	Cottonwood Creek	AC	10	empty	Shuman, 1943, notebook
1 June 1948	Karluk Lake outlet	DV	several	empty	Shuman, 1948, notebook
1 June 1948	Karluk Lake outlet	DV	2	sockeye smolt, DV fry	Shuman, 1948, notebook
8 Sept. 1949	Thumb	charr	few	salmon eggs	Crawford, 1949, notebook
summer 1953	Karluk Lake	charr	some	aquatic insects, salmon eggs	FRI, 1953, log book
1950–1953	Karluk, Thumb, and O'Malley River	charr	few	sockeye fry	Walker, 1954, report
10 May 1955	Karluk Lake outlet	charr	9	empty	Duncan, 1955, notebook
17 May 1955	upper Karluk River	DV	1	8 pink salmon fry	Nelson, 1955, notebook
22 June 1955	Karluk Lake outlet	DV	4	1–5 sockeye juveniles	Duncan, 1955, notebook
22 June 1955	Karluk Lake outlet	AC	1	sockeye juveniles	Duncan, 1955, notebook
23 June 1955	Karluk Lake outlet	charr	10	sockeye fry	Conkle, 1955, notebook
July–Oct 1955	Karluk Lake	charr	109	aquatic insects, SB and SB eggs salmon eggs, snails	Clark, 1965
7 June 1956	Karluk Lake outlet	charr	some	sockeye juveniles	Rabe, 1956, notebook
July–Aug. 1957	Moraine Creek	DV	many	salmon eggs	Greenbank, 1957, report
12 Apr. 1958	Karluk Lake outlet	charr	1	22 sockeye fry, aquatic insects	Raleigh, 1958, field notes
15 Apr. 1958	Karluk Lake outlet	charr	3	aquatic insects	Raleigh, 1958, field notes
5 Aug. 1959	Thumb beach	AC	5	salmon eggs	ABL, 1959, monthly report
spring 1967	Karluk Lake outlet	DV	some	sockeye smolt	Hartman et al., 1967

[1] AC = Arctic charr; DV = Dolly Varden.
[2] SB = Threespine stickleback.
[3] All notebooks, field notes, and reports located at NARA, Anchorage, AK, except FRI log book and Walker 1954 report located at FRI Archives, University of Washington, Seattle.

the "lake population" of Dolly Varden. Charr in the lake fed on aquatic insects, sticklebacks, stickleback eggs, snails, clams, sockeye eggs, and algae (Table 9-2). Barnaby believed that charr preyed on newly emerged sockeye fry each spring, but found little evidence they preyed on sockeye smolts in the river (Higgins, 1938):

At Karluk Lake it was noted that chars take a very heavy toll of red salmon fry in the spring at the time the young fish are entering the lake from the spawning streams. However, during the summer and fall relatively little damage is done to the salmon populations by these chars. They have been caught by means of seines and gill nets, and only rarely was one found that had been feeding on salmon fingerlings. Although

Table 9-3
Historic records of charr predation on sockeye salmon juveniles, Karluk Lake and River.

Date	Location	Charr[1]	Sockeye juveniles	Comment	Reference[2]
8 August 1900	hatchery nursery pond	DV	fry	64mm DV with 12 fry	Fassett, 1902
25 July 1903	hatchery corral	DV	fry	1 stomach with 5, 51mm fry	Rutter, 1903, field notes
26 June 1926	Karluk Lagoon	DV	76–102 mm young	1 stomach with several young	Rich, 1963
22 May 1934	S. Karluk Lake trib.	charr	fry	1 stomach with 12 fry	Barnaby, 1934, notebook
Aug–Sep 1935	Karluk Lake	AC	young	2 stomachs with young	DeLacy, 1941
May–Jun 1939	lower Karluk River	DV	smolt	1 stomach with 1 smolt	Morton, 1982
1939–1941	Karluk Lake	charr	young	5 stomachs with young	Morton, 1982
Apr 1940	Karluk Lake trib.	AC	fry	2 stomachs with 1 fry	Morton, 1982
Apr 1940	Karluk Lake trib.	DV	fry	2 stomachs with 1 fry	Morton, 1982
May–Jun 1940	lower Karluk River	DV	smolt	1 stomach with 8 smolt	Morton, 1982
May–Jun 1940	lower Karluk River	DV	smolt	1 stomach with 10 smolt	Morton, 1982
May–Jun 1940	lower Karluk River	DV	smolt	1 stomach with 2 smolt	Morton, 1982
1 June 1948	lake outlet	DV	smolt	1 stomach with 6 smolt	Shuman, 1948, notebook
1950–1953	Karluk, Thumb, and O'Malley River	charr	fry	small charr with 6–30 fry	Walker, 1954, report
22 June 1955	lake outlet	DV/AC	young	5 stomachs with 1–5 young	Duncan, 1955, notebook
22 June 1955	upper Karluk River	DV	fingerlings	DV predation observed	Duncan, 1955, notebook
23 June 1955	lake outlet	DV	fry	5 stomachs with fry	Conkle, 1955, notebook
3 June 1956	lake outlet	DV	small reds	DV feeding on small reds	Rabe, 1956, notebook
12 April 1958	lake outlet	DV	fry	1 stomach with 22 fry	Raleigh, 1958, notebook
Spring 1967	lake outlet	DV	smolt	DV predation seen at night	Hartman et al., 1967
1982	lake outlet	charr	fry	1 stomach with fry	Wilmot et al., 1983, report
May 1983	upper Karluk River	charr	fry	95 stomachs with 93 fry	McIntyre et al., 1988
May 1983	Thumb River and beach	charr	fry	13 stomachs with 59 fry	US FWS, 1985, report
Apr–May 1984	upper Karluk River	charr	fry	128 stomachs with 2490 fry	US FWS, 1985, report
June 1984	upper Karluk River	charr	fry	9 stomachs with 3 fry	US FWS, 1985, report
June 1984	lake outlet	charr?	smolt	predation observed at dusk	US FWS, 1985, report
May 1985	upper Karluk River	charr	fry	485 stomachs with 4879 fry	McIntyre et al., 1988
May 1986	upper Karluk River	charr	fry	571 stomachs with 2570 fry	McIntyre et al., 1988

[1] AC = Arctic charr; DV = Dolly Varden
[2] All notebooks located at NARA, Anchorage, AK. Rutter 1903 field notes located at California Academy of Sciences Archives, San Francisco, CA. Walker (1954) report located at FRI Archives, University of Washington, Seattle. Wilmot et al. (1983) report from Richard L. Wilmot, Auke Bay, AK. US FWS 1985 report located at ARLIS, Anchorage, AK.

> salmon eggs do comprise a large part of the diet of these fish, it was noted that the chars were feeding almost entirely on floating eggs displaced by the spawning activities of the salmon and these eggs would die whether they were eaten or not. An analysis of stomach contents of chars in Karluk River showed that the chars in the river were not feeding on seaward migrants.

It is unclear why he claimed that charr preyed heavily on fry since he only noted this once in the creeks entering the south end of Karluk Lake on 22 May 1934 (Table 9-3). There, he checked several charr caught by bear hunters and found that one charr had eaten 12 sockeye fry. When Barnaby left Karluk's research project in June 1938, he turned over all of his 1935–37 data on charr food habits to DeLacy. Barnaby's early food habits work helped initiate Morton and DeLacy's charr research of 1939–41.

Morton and DeLacy's Studies of Charr Food Habits (1939–41)

Morton and DeLacy completed the first detailed study of charr food habits at Karluk during 1939–41, testing the common belief that charr were serious predators of sockeye eggs and juveniles. Their studies were noteworthy because, for the first time, both charr species were clearly identified and thousands of stomach contents were examined from April to September over three years. Further, they sampled charr from a wide range of habitats—Karluk River, littoral and limnetic zones of Karluk Lake, tributary streams, and ocean near Karluk Spit and Larsen Bay. They also used a wide range of collecting gear, including beach seines, gill nets, fyke nets, hook-and-line, weir traps, and commercial ocean traps. The study examined both up- and down-migrating Dolly Varden and charr in streams with and without spawning sockeye salmon.

Despite examining thousands of charr stomachs from the Karluk ecosystem, few contained juvenile sockeye (DeLacy, 1941; Morton, 1982). When DeLacy combined his 1939–40 food habits data with past studies by Rutter in 1903 and Barnaby in 1935–36, juvenile sockeye occurred in only 9 Dolly Varden stomachs of 3,371 examined and in only 3 Arctic charr stomachs of

Allan DeLacy (left) and William Morton (right), Camp Island cabin, Karluk Lake, 1939–40. (William M. Morton, from Robert S. Morton, Portland, OR)

2,155 examined. Likewise, in Morton's 1939–41 study, juvenile sockeye occurred in only 9 Dolly Varden of 3,983 examined and in only 1 Arctic charr of 1,992 examined. Of the 9 Dolly Varden with juvenile sockeye, 4 (predator size, 520–600 mm) had consumed 1–10 sockeye smolts in May–June. Only 42 charr stomachs of 5,975 examined by Morton had sockeye, coho, or pink salmon juveniles. Based on these results, charr predation on Karluk's juvenile salmon appeared to be insignificant.

Some biologists questioned Morton and DeLacy's results, and even DeLacy (1941) urged caution. First, they examined no charr in fall and winter months (October–March), which left the possibility of additional predation during that period. Second, they examined few charr in early spring when sockeye fry emerged and migrated to the lake. DeLacy purposely visited Karluk Lake in early April 1940 to check on this possibility, but, unluckily, the previous winter had been milder than usual and the fry migration had already occurred before his visit. Sockeye fry occurred in only 2 Dolly Varden and 2 Arctic charr of 456 examined in April 1940. Third, questions arose whether the previous predator control program had abnormally depressed Dolly Varden populations at Karluk, causing their food habits study to be done at a time of unusual ecological conditions and atypical predator-prey interactions. A final problem with the food habits study was that it remained unpublished for 40 years and unknown to many biologists (Morton, 1982).

In contrast to the sparse predation on juvenile sockeye salmon, Morton and DeLacy documented that both charr species readily ate sockeye eggs in June–September (Table 9-2). For example, sockeye eggs were present in 642 Dolly Varden of 2,565 examined and in 421 Arctic charr of 1,992 examined at Karluk Lake during 1939–41. But the question remained, did egg consumption by charr decrease sockeye abundance? Since there was little chance that unburied and drifting eggs survived to hatching, Morton and DeLacy viewed this egg consumption as a scavenging behavior, not predation, and unlikely to reduce sockeye numbers:

> [Karluk Lake, 1939–1941] Some observers have expressed the belief that the Dolly Varden would dig salmon eggs out of the gravel, if necessary, to obtain them for food. Such activity has never been observed by this writer, and at Karluk Lake it would be unnecessary because of the large number of salmon eggs drifting downstream during the peak of the red salmon spawning activity. These drifting eggs had been dislodged by new spawners digging new redds over areas seeded by earlier arrivals. . . . I saw quarts of red salmon eggs massed behind large boulders in spawning streams. . . . An actual count from a pint of salmon eggs taken from charr stomachs in 1939 indicated that 17% of the eggs were 'eyed'. A similar quantity of drifting eggs from the same stream at the same time when counted indicated that 20% of them were eyed. It was concluded that the feeding on eggs was a 'scavenger' action and could not in any sense be considered a 'predatory' one, as practically all of these unburied eggs were doomed to destruction whether or not they were consumed. (Morton, 1982)

> [Concerning charr at Karluk Lake, 1939–1941] It cannot be assumed . . .that each salmon egg which the fish eat represents the destruction of a potential salmon. For instance, the chars, particularly *S. alpinus*, which lie in schools off the mouths of the lake's tributaries, feed on red-salmon eggs and other food material that drift into the lake. Observations have shown that a large percentage of these drifting eggs are either dead or infertile. . . . Drifting salmon eggs are also eaten by the Karluk chars, especially *S. malma*, which inhabit the Thumb and O'Malley river systems during the red salmon's spawning season. Here again, however, there is little reason to believe that a significant proportion of the eggs which are eaten would eventually hatch and produce salmon fry and fingerlings. . . . A drifting egg which lodges on the surface of the stream bed may be assumed to be much more susceptible to destruction by fungus, temperature extremes, sunlight, floods, or droughts than is an egg which is properly buried in the gravel. (DeLacy, 1941)

Morton and DeLacy found that food preferences varied seasonally in both charr species. In April–May, Dolly Varden and Arctic charr primarily fed on aquatic insects, snails, and leeches. In May–June, about 80–90% of down-migrating Dolly Varden had empty stomachs, and those with food had eaten aquatic insects. Similarly in July, up-migrating Dolly Varden had empty stomachs. Down-migrating Dolly Varden were emaciated after spending the winter in the lake, while up-migrating Dolly Varden were plump after feeding for several weeks in the ocean. In June–September, Dolly Varden and Arctic charr ate many sockeye eggs and aquatic insects. Arctic charr fed heavily on sticklebacks and stickleback eggs in the lake in June–July, but Dolly Varden seldom ate these foods. In July–September when salmon carcasses were common, Arctic charr ate decomposing salmon flesh and associated blowfly larvae; few Dolly Varden ate salmon flesh. Dolly Varden fed on small marine fishes and crustaceans in the ocean in June–July, this food powering rapid grow and improved condition. In summary, the major foods that contributed to Dolly Varden growth were marine fishes and crustaceans, freshwater aquatic insects and invertebrates,[24] and sockeye salmon eggs. The major foods of Arctic charr were aquatic insects and invertebrates, sockeye salmon eggs, decomposing salmon flesh, and sticklebacks and their eggs.

In conclusion, Morton and DeLacy found that Dolly Varden and Arctic charr predation on Karluk's juvenile sockeye salmon was insignificant. They judged that charr consumption of sockeye salmon eggs was an unharmful scavenging behavior. These results challenged the long-held belief that charr were severe predators of sockeye salmon and also helped to curtail the predator control efforts of destroying Dolly Varden at the Karluk River weir.

Charr Food Habits (1940s–1960s)

Morton and DeLacy's results showing negligible charr predation on juvenile sockeye failed to convince some biologists, though none doubted that charr ate many sockeye eggs. After years of condemning charr as serious salmon predators, biologists found it difficult to accept this new evidence—the results seemed just too good. Instead, they began to wonder if charr predation on juvenile sockeye might be concentrated at specific times and places that were missed in the previous study. Fry emergence and migration to the lake seemed to be a vulnerable period of the life cycle, and field evidence indicated that charr congregated at creek mouths or near the lake's outlet each spring awaiting newly emerged fry. Further research seemed to be justified to fully understand the charr-sockeye interaction. Therefore, biologists continued to examine charr stomachs for evidence of sockeye predation after 1941. Though seldom part of the year's planned research, this work occurred sporadically and involved few charr specimens (Tables 9-2 and 9-3). Of course, another reason to continue these studies after 1941 was that Morton and DeLacy's work remained unpublished and largely unknown.

Willis Rich recommended in 1946 that Shuman expand the Karluk Lake studies to include the "stickleback-Dolly Varden-red salmon biome," and the FWS did initiate studies of sticklebacks, limnology, and sockeye salmon, but not of charr.[25] Nevertheless, Shuman occasionally examined charr stomachs during 1943–49, but his results generally matched the previous study. He examined a 390 mm Dolly Varden in the river below the lake's outlet on 1 June 1948 that had eaten six sockeye salmon smolts, this suggesting a possible time and place of significant predation. Since Shuman believed that charr and stickleback populations were inversely related, he declared that "one method of control of sticklebacks may be that of encouraging the propagation of charrs, particularly the arctic form."[26] Perhaps Shuman was the only biologist in Karluk's research history to suggest that charr numbers needed to be enhanced, rather than destroyed.

FRI biologists also examined charr stomachs at Karluk during 1948–55, but their work remained unpublished.[27] Walker incidentally collected many charr while beach seining at the lake during 1950–54 and examined some for their diet. His findings of generally

[24] To identify insect and other invertebrate foods found in charr stomachs, Morton sent specimens to several specialists and documented the presence at Karluk of the caddisflies *Glossosoma alascense*, *Chyranda centralis*, *Clistoronia magnifica, Psychoglypha subborealis, Hesperophylax alaskensis, Radema stigmatella,* and *Ecclisomyia conspera*; leeches *Glossiphonia complanata mollissima* and *Erpobdella punctata; and* mollusks *Sphaerium tenue, Pisidium liljeborgii, Menetus planilatus, Valvata leivisii helicoidea,* and *Lymnea atkaensis* (Denning, 1951; Moore and Meyer, 1951; Morton, 1982).

[25] Letter (16 August 1946) from Willis H. Rich, Consultant, Salmon Fisheries Investigations, Stanford University, to R. F. Shuman, FWS, Seattle. Located at NARA, Anchorage, AK.

[26] See footnote 19.

[27] Letters (18 April and 30 May 1997) from Allan C. Hartt, Coupeville, WA, to Richard L. Bottorff, South Lake Tahoe, CA. Some of the charr food habits data may be present in FRI field notebooks, located in the FRI Archives, University of Washington, Seattle.

minor charr predation on sockeye juveniles agreed with those of Morton and DeLacy, but he also indicated specific times and places where it might be intense:

> [Speaking of charr predation on Karluk's juvenile sockeye, 1950s] Under natural conditions no extensive predation on any age group of the young reds has been found. However, that does not preclude the existence of such. Small Dolly Varden, three and one-half to seven inches [89–178 mm], taken in red sampling gear at the same time as fry, have contained from six to thirty of these fish. This was noticed in the Karluk, Thumb and O'Malley Rivers. Larger sized dollies captured at the mouths of Thumb and O'Malley Rivers and in the lake at Camp Island and the outlet during May and June did not contain reds of any size. However, a small minority of these same sized fish in the Karluk River did have fry . . . No predation on the fingerling by the other fishes has been noted. . . . In summary, it would seem that the fry at the time of emergence and shortly thereafter do undergo considerable predation, but the fingerling do not.[28]

Walker's report that small charr ate sockeye salmon fry must be viewed with caution since some of this feeding may have occurred while predators and prey were unnaturally confined within beach seines.

Associated with Karluk's research program, FWS biologists Clark Thompson and Charles Huver studied Dolly Varden at Bare Lake during 1954–55, including population estimates, size distributions, movements within the lake, and comparative food habits of 48 Dolly Varden and 51 juvenile sockeye.[29] Dolly Varden fed in summer on caddisfly larvae, winged insects, sticklebacks, stickleback eggs, snails, pea clams, chironomid larvae, salmon eggs, and juvenile sockeye. Little predation on juvenile sockeye occurred in most areas of the lake, but at the shallow outlet Dolly Varden preyed on schools of sockeye smolt that gathered for their seaward migration and on younger juveniles whenever present. Twenty Dolly Varden at the outlet in June 1955 ate on average 0.5 sockeye smolts and three coho juveniles. Predation increased when the young sockeye were unnaturally confined in the outlet's fish trap. Intermediate-sized Dolly Varden (230–300 mm) accounted for most of the predation on young sockeye; larger fish consumed other foods.[30] Winter foods of four Dolly Varden taken through the ice in 1955 included sticklebacks, caddisfly larvae (one individual had 118 larvae), chironomid larvae, ostracods, and other aquatic insects.

FWS seasonal biologist T. O. Duncan saw charr preying on juvenile sockeye salmon above the outlet weir in June 1955. Nine charr examined in early May had empty stomachs, but those checked in mid June contained young sockeye:

> [Karluk River at lake's outlet, 22 June 1955] I caught four dollys and one charr, all of which had red salmon fingerlings in the stomach, at least one, and as many as five . . . since the weir was put in early, the dollys didn't get a chance to get out of the lake (or were late) and this caused them to prey on the fingerlings, because of hunger. There was evidence of predation just by watching the fish (Dollys) taking the fingerlings in the river above the weir. The fingerlings would break water and larger fish (Dollys) would swirl (in numbers) in the same area. Case closed—Dollys guilt[y] of predation at present! What % is guilt[y] is another question, but it is quite a large sum from my observation. Incidentally, the char (taken on lure) had 4 fingerlings in the stomach. On the 20% return to spawn index, that's one less spawner in the future! (Theoretically speaking!).[31]

Significantly, his observations record a time and place when charr predation might be intense, though it is unclear which juvenile life stage was being eaten (newly emerged fry, intermediate-sized young, or smolts).

FWS wildlife biologist Webster Clark (1965) examined 109 charr at Karluk Lake in July–October 1955, finding that they had eaten aquatic insects, snails, sticklebacks, stickleback eggs, and salmon eggs, but no juvenile sockeye. At the lake's outlet, 25% of the charr had empty stomachs, but in or near lake tributaries, about 30% had sockeye eggs. One large charr (1 kg) had eaten 1,020 salmon eggs. Clark's food habits results agreed with those of Morton (1982) and DeLacy (1941).

In 1958 Rounsefell published his influential analysis of the reasons for the decline in Karluk's sockeye salmon. Believing that fish predation had reduced sockeye salmon numbers, he strongly recommended removal of "all predator species of fish from Karluk Lake and its tributaries." The force of his recommendation renewed interest in the charr-sockeye interaction and the possible value of controlling charr populations at Karluk. Charles Connelley, FWS fishery manage-

[28] Walker, Charles E. 1954. Karluk young fish study, 1950–1954. Kodiak Island Research, FRI, University of Washington, Seattle. Unpubl. report. Located at FRI Archives, University of Washington, Seattle, WA.

[29] Thompson, Clark S. ca. 1963. Studies of the Dolly Varden (*Salvelinus malma* Walbaum) at Bare Lake, Alaska. FWS, Montlake Laboratory, Seattle, WA. Unpubl. report. 17 p. Located in the personal papers of Clark S. Thompson, Shelton, WA.

[30] Charles W. Huver, Forest Lake, MN, personal commun. with Richard L. Bottorff, 1998.

[31] Duncan, T. O. 1955 notebook. Located at NARA, Anchorage, AK.

ment supervisor for the Kodiak area, restated in 1958 the historic belief that Dolly Varden preyed heavily on juvenile sockeye and recommended an experimental control program:

> [Karluk River, 1958] Dolly Varden trout constitute a normal peril to salmon smolts here as elsewhere. Nevertheless, it is suggested that a controlled experiment be run at Karluk, seining dollies at the river mouth when they are concentrating on the smolt migration. It is believed that by depressing their numbers during this time the Dolly Varden depredations can be greatly decreased at a time when smolt protection may do the most good, immediately before entering the ocean constant. It has been observed at Chignik and elsewhere that Dolly Varden are heavily concentrated in the river mouth during smolt migration and that they apparently do feed heavily and almost exclusively on the migrants.[32]

In spite of these sentiments, the impact of charr predation on sockeye salmon numbers remained controversial during this period. In particular, Philip Nelson remained unconvinced that charr predation was severe, his beliefs being based on 11 field seasons of research at Karluk:

> [Discussing charr predation at Karluk Lake, 1946–1956] In regard to the Dolly Varden and Arctic Char studies by DeLacy and Morton I am in general agreement with their conclusions. I have seen no signs of heavy predation on juvenile red salmon by these species. I am quite convinced that the situation at Karluk is in no way comparable to that in Bristol Bay . . .[33]

Because of Rounsefell's ideas about predatory fishes, FWS biologist John Greenbank studied Dolly Varden food habits at Karluk Lake in 1957, in particular trying to understand charr consumption of sockeye eggs.[34] He found that before adult sockeye salmon reached the lake each spring, small Dolly Varden in the tributary creeks fed on aquatic insects, but as sockeye spawning began these charr increasingly ate salmon eggs. To observe this dietary shift, Greenbank collected 30 small Dolly Varden daily from a single pool of Moraine Creek (15 July–16 August). During this period, several groups of adult sockeye entered the creek, spawned, and died, giving a wide range of salmon egg availability. About 60–95% of Dolly Varden ate salmon eggs when sockeye actively spawned in July, but less than 20% ate eggs as spawning declined in August. The number of eggs per Dolly Varden stomach varied directly with spawning activity, ranging from 1 to 133 (mean 17). Although Greenbank examined more than a thousand Dolly Varden stomachs, he never mentioned that he found juvenile sockeye. Believing that his 1957 studies duplicated Morton and DeLacy's previous work, he repeated their conclusions. Nevertheless, he also felt that his food studies were incomplete and recommended further research during winter months, spring fry emergence, and smolt migration.

Greenbank particularly wanted to resolve the question of whether egg consumption was a predatory or scavenging behavior and designed an ambitious field experiment to measure sockeye egg deposition and fry production in two creeks, one with and one without Dolly Varden:

> [Karluk Lake, 1957] Such an experiment might produce, indirectly, some sort of an answer to the much debated question as to whether the eggs eaten by the Dolly Vardens are eggs which would have sunk in the gravel, and thus have produced fry, or whether they are "floaters", perhaps infertile, which would have been wasted. . . . It is almost impossible to answer this question by direct observation. Dolly Vardens have been seen in the immediate vicinity of spawning female red salmon. But in the stirring up of the water when the egg-laying takes place, it is difficult to tell whether the dolly's are grabbing eggs as they are being extruded. On the other hand, free floating, or rather rolling, eggs are to be found in the stream, and these may be the ones upon which the dolly's mainly are feeding.[35]

Although an interesting idea, the FWS never pursued Greenbank's experiment, but did list it in a research plan for the 1958 field season, which also included an effort to control charr at times of intense predation in the upper Karluk and Thumb rivers.

Associated with Greenbank's 1957 study, FWS seasonal biologist John McNair measured the digestion rate (at 14°C) of sockeye eggs in Dolly Varden. He starved a group of Dolly Varden (180–280 mm) for several days and then fed them as many eggs as they would eat. By periodically examining their stomach contents over the next 65 hours, digestion rates were measured. Eggs remained intact in the stomach for the first 24 hours, but then began to disintegrate until all had digested by 60–65 hours.

In 1958 FWS biologists Charles Conkle and Robert Raleigh tried to determine if charr preyed on newly

[32] Connelley, Charles F., Jr. 1958. Alaska commercial fisheries annual report, Kodiak area, 1958. U.S. Department of the Interior, FWS. Unpubl. report. 29 p. Located at ABL Library Files, Auke Bay, AK.
[33] See footnote 18 (4).
[34] Greenbank, John T. 1957. Dolly Varden studies, Karluk Lake, 1957. Field Report (1 October 1957). Unpubl. report. 11 p. Located at NARA, Anchorage, AK.

[35] See footnote 34.

emerged sockeye fry. Although the biologists reached Karluk Lake on 7 April, they found few live eggs buried in the substrate and few fry in the tributary creeks or lake's littoral since fry emergence and migration had already occurred. As for DeLacy in 1940, a mild winter had advanced the 1958 fry migration. No schools of predatory charr awaited the fry at creek mouths. Raleigh concluded that "from the limited number of Dolly Varden stomachs examined to date, there does not seem to be any excessive predation taking place on the fry except possibly within the Karluk River."[36] Most Dolly Varden in the upper river had empty stomachs, but a few did contain sockeye fry:

> [Karluk River near lake's outlet, 12–15 April 1958] Went fishing at 5pm. Caught one large dolly. Its stomach contained 22 red fry & 2 diptera . . . From our limited sampling I would say that there is not a large concentration of dollys in or around the streams. Further that the lake resident dollys are not feeding on red fry but the river resident dollys are feeding heavily on them . . . Went fishing for a half hour this evening. Cy and I caught 3 dollys. We examined their stomachs. All three were feeding on diptera larva, no fry.[37]

After the charr predation studies of 1957–58, Karluk biologists spent little further effort on the topic for many years. Raleigh used SCUBA in August 1959 to observe spawning sockeye at Thumb Beach and found five nearby Arctic charr with 166 salmon eggs in their stomachs.[38] In the 1960s, Drucker reported intense charr predation on sockeye smolts at the lake's outlet in early spring (Hartman et al., 1967).

Charr Predation on Juvenile Sockeye in the Upper Karluk River (1980s)

FWS biologists conducted a detailed study of charr predation on juvenile sockeye salmon during 1982–86; this was part of a larger research program to determine why Karluk's sockeye runs had declined (McIntyre et al., 1988).[39] Beginning in 1982, fish were regularly collected from many littoral sites around Karluk Lake using beach seines, gill nets, and hook-and-line. The sampling effort was expanded in later years to also include the lake's limnetic zone and upper Karluk River. The fish captured included charr (Dolly Varden and Arctic charr were not separated), sockeye and coho salmon juveniles, threespine sticklebacks, and coastrange sculpins. This large sampling effort showed that newly emerged sockeye fry first migrated to the lake's littoral in late May to mid July, followed by movement to the limnetic zone. Similar to Morton and DeLacy's results, charr from the 1982 samples (mainly from lake beaches and creek mouths) had eaten sockeye eggs, but few had preyed on juvenile sockeye.

Before concluding that charr predation was trivial at Karluk, the FWS decided to focus their next study on the specific times and places where predation might be important. Charles Meacham, ADFG research supervisor, had suggested this possibility based upon his experiences in the Wood River system, Alaska. Since newly emerged sockeye fry seemed vulnerable to predation, in 1983 the FWS collected charr from the upper Karluk River near the lake's outlet and for a short distance (2.5 km) downstream. Most charr in this river section were Dolly Varden of moderate to large size (357–588 mm fork length). Biologists examined the charr foods by flushing the stomach contents of live fish into a container using a small pump. Sampled charr were tagged and released back into the river alive. As suspected, charr in the upper river in April–May had preyed on sockeye fry migrating toward the lake. For example, 93 fry were eaten by 27 of 95 charr examined in May 1983. Higher predation rates occurred in 1984 (26 April–12 May), with 2,490 fry being eaten by 60 of 128 charr examined. By late May and June, not many charr were still present in the upper river and those examined had few sockeye fry.

The FWS again measured charr predation on sockeye fry in the upper Karluk River in the spring of 1985 and 1986. In 1985, 485 charr ate 4,879 fry, and in 1986, 571 charr ate 2,570 fry (McIntyre et al., 1988). In total for 1983–86, 1,279 charr ate 10,032 fry. Clearly, intense charr predation on fry occurred in the upper river for several weeks each spring, a noticeably different result than found by Morton (1982) and

[36] Raleigh, Robert F. 1958. Karluk Lake field reports (4 April–7 June 1958). FWS, Karluk Lake, AK. Six unpubl. reports. Located at NARA, Anchorage, AK.

[37] Raleigh, Robert F. 1958 notebook. Located at NARA, Anchorage, AK.

[38] BCF. 1958–1960. Monthly research report. U.S. Department of the Interior, FWS, BCF, Alaska Region. Unpubl. reports. Located at ABL Office Files, Auke Bay, AK.

[39] 1) Wilmot, Richard L., Carl V. Burger, David B. Wangaard, James W. Terrell, and Robert M. Lichorat. 1983. Karluk Lake studies, progress report. USFWS, Alaska Field Station, National Fishery Research Center, Anchorage, (July 1983). Unpubl. report. Copy from Richard L. Wilmot, ABL, Auke Bay, AK. 2) USFWS. 1985. Karluk Lake sockeye salmon studies 1984. Part I: Competition, predation, and lake fertility. Part II: Karluk Lake smolt outmigration–1984. Draft. USFWS, Seattle National Fishery Research Center, Alaska Field Station. (January, 1985). Unpubl. report. 39 p. Copies located at ADFG Office Files, Kodiak, AK, and ARLIS, Anchorage, AK.

DeLacy (1941). The FWS results confirmed growing anecdotal evidence of springtime charr predation in the upper river.

Associated with these charr food studies, FWS biologist James Finn tagged and released many Dolly Varden to learn if individual fish remained in the upper river for long periods to prey on fry or quickly moved through this area as they migrated downstream to the ocean. Surprisingly, Finn rarely recaptured a previously tagged Dolly Varden, showing that they rapidly moved through the upper river.[40] Thus, a continually changing group of Dolly Varden preyed on the sockeye salmon fry, not the same group that remained near the outlet for weeks.

In contrast to the results for the upper river, the FWS found minimal charr predation on juvenile sockeye at most Karluk Lake sites during 1982–86. Limited predation occurred at Lower Thumb River and Thumb Beach in May 1983, but aquatic insects were typically the most common charr foods at the majority of lake sites, not fry.[41] Since charr were seldom captured in the limnetic zone, severe predation seemed unlikely once juvenile sockeye reached this open-water rearing habitat. Thus, charr predation on juvenile sockeye was insignificant at most Karluk Lake locations.

The FWS found little evidence during 1982–86 that charr preyed on sockeye smolts in the upper Karluk River, there being relatively few charr present during peak smolt migration. And yet, as smolts moved from the lake into the upper river in early June 1984, reportedly "large salmonids (≥400 mm) were observed rushing through these schools of smolt and were apparently feeding on them."[42] These observations prompted the FWS to plan further studies of charr predation on sockeye smolts in 1985–86, but this work was not done.

The FWS studies at Karluk during 1982–86 were also noteworthy in focusing attention on the predation of sockeye fry by juvenile coho salmon (McIntyre et al. 1988).[43] Previously, a few Karluk biologists had mentioned that juvenile coho preyed on young sockeye, but the extent of this behavior was unexplored. Barnaby confined sockeye salmon fry in a small creek at Karluk in May 1931 and found them missing in July, causing him to surmise that "the thousand red fry I put in there made pretty good food for the silvers I guess."[44] The FWS found during 1982–86 that small juvenile coho (<80 mm fork length) preyed little on young sockeye, but larger juvenile coho (>80 mm) had higher predation rates (McIntyre et al., 1988). Of 5,013 large juvenile coho examined, 1,410 sockeye fry had been eaten. For the 5-year study, juvenile coho averaged 0.08–0.74 sockeye fry per stomach, and the predation rate increased with prey density. Most predation occurred in June and early July when coho and sockeye salmon young inhabited the same shallow waters along the lake's shorelines and near creek mouths. As sockeye fry left the littoral by late July, coho predation declined. Although the overall coho predation of sockeye fry was low at most lake sites, it was significant at Thumb River, where often 50% of juvenile coho had eaten sockeye fry.

Unusual Charr Observations

Associated with the topic of charr predation, Karluk's fisheries literature contains a few unusual observations. In a surprising turnabout, Clark found charr in the stomachs of three spawning sockeye salmon in Karluk's tributaries in 1952.[45] During this same period, several biologists observed river otters catching and eating charr in the upper river.[46] They also found charr in bald eagle nests at Karluk Lake, though it was unclear if the eagles had preyed on or scavenged these fish. Nelson and Carlson saw mergansers catch Dolly Varden (as large as 200 mm) at the upper river weir.[47] Morton (1982) found juvenile charr in three Arctic charr stomachs at Karluk Lake and believed that this cannibalism indicated Arctic charr might be worse predators of young sockeye than Dolly Varden. Shuman also found a charr fry in the stomach of a 390 mm Dolly Varden in the upper river.[48]

Owen observed an odd Dolly Varden behavior at the 1958 counting tower on the upper Karluk River.

[40] James E. Finn, Anchorage, AK, personal commun. with Richard L. Bottorff, 1997.

[41] See footnote 39.

[42] See footnote 39.

[43] See footnote 39.

[44] Barnaby, J. Thomas. 1931 notebook (18 May and 28 July). Located at NARA, Anchorage, AK.

[45] Lindsley, Roy R. 1952. Annual report, Kodiak area, 1952. FWS, Branch of Alaska Fisheries. Unpubl. report. 27 p. Located at ABL Library File, Auke Bay, AK, and at NARA, Anchorage, AK.

[46] 1) See footnote 28.
2) Duncan, T. O. 1955 notebook (26 May).
3) Crawford, John S. 1949 notebook (23 and 29 May)
4) Reeves, J. D. 1954 notebook (5 June). All notebooks located at NARA, Anchorage, AK.

[47] 1) Nelson, Philip. 1955 notebook (3 October).
2) Carlson, Robert. 1956 notebook (1 September). Both notebooks located at NARA, Anchorage, AK.

[48] Shuman, Richard F. 1948 notebook (1 June). Located at NARA, Anchorage, AK.

Here, many Dolly Varden accumulated just downstream from white panels placed on the river bottom to aid biologists in seeing and counting migrating salmon. The Dolly Varden aligned themselves in regular rows across the river. On closer examination the fish appeared to flare their pectoral fins ventrally, with the tips touching the substrate, as if they were braced against the river's current.[49]

Conclusions on Charr Predation

Ever since Karluk's salmon canneries began operating in 1882, dramatically different opinions have been held about the severity of charr predation on juvenile sockeye salmon. For the first 60 years, all charr were called Dolly Varden and it was commonly believed that they were ravenous sockeye predators. This belief was not based on direct evidence from Karluk. In 1939 Karluk's charr were discovered to be two species, Dolly Varden and Arctic charr, each with its own food preferences, habitats, and migratory behaviors. The first comprehensive food study of Karluk's charr during 1939–41 found little evidence of predation on young sockeye, but large consumption of sockeye eggs. Biologists then suggested that charr may be beneficial to sockeye salmon by preying on sticklebacks, which potentially competed with young sockeye. For the next 45 years, charr were thought to be insignificant predators of young sockeye, except for Rounsefell's claim in 1958 that sockeye runs at Karluk might be restored by controlling fish predators. Further studies at Karluk during 1982–86 confirmed previous conclusions that charr predation on young sockeye was generally insignificant, but may be intense at specific times and places.

The specificity of charr predation reinforces a unifying theme of many life history and ecological questions concerning sockeye salmon and other fishes at Karluk. To fully understand the charr-sockeye interaction, food studies were needed from many different habitats and seasons. Broad generalizations based on data from a few times and places resulted in the wrong conclusions. Thus, the topic of charr predation highlights the great variability and diversity that are paramount features of the Karluk Lake ecosystem.

Despite the present understanding of charr predation at Karluk, research questions remain, including: 1) what is the full range of specific times and places of intense predation on young sockeye? and 2) what are the ultimate effects of predation losses on sockeye salmon abundance? Answers to these questions are incomplete, especially since the total populations of Dolly Varden and Arctic charr remain unknown at Karluk. Uncertainties also exist about the extent of charr predation during winter.

Consumption of Sockeye Salmon Eggs

All charr food studies at Karluk, plus many direct field observations, document that Dolly Varden and Arctic charr consume many sockeye eggs during the spawning season. Salmon eggs are important and predictable food resources for both species, which seasonally gather in or near salmon spawning habitats. The main question about this egg consumption is whether charr are eating surplus eggs that are unlikely to survive because they were not buried in the gravel substrates, or whether charr are taking eggs directly from the redd as the female extrudes them and before the eggs are buried in the substrate. The consensus viewpoint is that charr mainly scavenge eggs unlikely to survive; this feeding behavior probably has no impact on sockeye salmon abundance. Quite likely, egg consumption is both a scavenging and predatory behavior.

Predation on Newly Emerged Sockeye Salmon Fry

Newly emerged sockeye fry have always been considered vulnerable to charr predation as they migrate to Karluk Lake. Food studies confirm this view for specific times and locations, but at many lake tributaries and beaches, predation appears to be negligible. Significant charr predation occurs in the upper Karluk River just below the lake's outlet from late April to mid May as fry move toward the lake. But the significance of this predation for sockeye salmon abundance remains unknown. Other places and times of heavy predation, as yet unknown, may exist in the Karluk system (e.g., Lower Thumb and O'Malley rivers). Several biologists visited Karluk Lake in early spring to observe the fry migration and possible charr predation, but often arrived too late. Charr aggregations at creek mouths during spring suggested that these fish awaited migrating sockeye fry and that predation may have been intense. Of course, predation studies in early spring are often difficult because of the harsh weather and ice-covered lake.

[49] John B. Owen, Grand Forks, ND, personal commun. with Richard L. Bottorff, 1997.

Predation on Sockeye Salmon Juveniles in the Limnetic Zone of Karluk Lake

Apparently, charr seldom prey on juvenile sockeye once they reach their rearing habitat in the limnetic waters of Karluk Lake. Yet some caution is justified about this conclusion, since past studies of charr foods seldom mention the size of young sockeye eaten; instead, prey were defined by ambiguous terms such as “fry,” “fingerlings,” and “parr.” Thus, the exact habitat where charr predation occurred often remains unclear.

Predation on Sockeye Salmon Smolts

Only sparse or anecdotal evidence exists about charr predation on sockeye salmon smolts at Karluk. Since Arctic charr rarely inhabit the Karluk River, they have little chance of preying on smolts once the migrants leave the lake. Dolly Varden and sockeye smolts migrate down the Karluk River each year in May–June, and this close juxtaposition of the two species would seem to favor intense predation. Yet the peak migration for Dolly Varden occurs a week or two before that of the sockeye smolts, and most down-migrating Dolly Varden examined in the lower river have empty stomachs. These fish often are emaciated after their long winter residence in the lake. If predation does occur, most observations indicate that it happens as smolts leave Karluk Lake, this being particularly noticeable during 1945–75 when the Karluk River weir was located near the lake’s outlet. The weir, being an unnatural confining structure in the river, possibly increased predation on smolts as large schools accumulated upstream. Sockeye smolts may also be preyed upon as they enter the lagoon or ocean at Karluk Spit, but few data support this claim.

CHAPTER 10

Brown Bear Predation on Sockeye Salmon

We thought we knew about predation, but in reality we only felt.–D.L. Allen, 1954

Few events are more dramatic than the scene of a brown bear pouncing on a spawning sockeye salmon and carrying the hapless, struggling creature off to the bank to devour it while an army of screaming gulls waits impatiently for the leftovers. After seeing such an event, many observers would think that there would be more salmon to catch if we eliminated or greatly reduced the number of bears. No observer would deny the fact that brown bears consume a large number of sockeye salmon when both predator and prey come together on the latter's spawning ground. But whether or not control of the predator would result in an increased number of the prey is not at all clear. The answer depends at least in part on the situation, as we will see in the paragraphs that follow.

Observations of Bear Predation at the Karluk River System Before 1947

Although the first humans to observe a brown bear catch and eat a sockeye salmon in the Karluk River System were the Alutiiq people many thousands of years ago, perhaps the first biologist to witness and document this act was Tarleton H. Bean who visited Karluk Lake in 1889 and wrote: ". . . Goolia's [his guide's] sharp eye discovered a grizzly with two cubs crunching a salmon. . . " (Bean, 1889). During the same trip Bean described the manner in which bears catch and eat salmon: "Bears consume large quantities of the breeding fish. They may be seen standing at the edge of the stream, where the water is shallow, and occasionally striking salmon with their claws and throwing them on the shore, where they are eaten alive" (Bean, 1891). Many authors have reiterated this observation. However, Troyer and Hensel[1] described how bears capture salmon somewhat differently: "They locate salmon visually and immediately pounce with forefeet to pin their quarry to the bottom. The immobilized fish is then clenched in the teeth and taken to a gravel bar or stream bank for ingestion." The senior author has observed this process many times and corroborates the Troyer and Hensel interpretation.

During the 56-year period following Bean's visit to Karluk Lake, many other anecdotal references concerning bear predation on sockeye salmon appeared in the field notes and publications of Karluk investigators (Table 10-1). Most of the observations were made during general surveys of the stream and lake margins because no serious investigations of bear predations were undertaken prior to 1947. Many of the observers were impressed by the magnitude of the bear predation they saw, but none so much as Shuman who estimated that 25 to 33% of the sockeye salmon spawning population was consumed by bears in 1943. Shuman did not state how he arrived at those figures.

On the other hand, in the two monumental publications of the period, Gilbert and Rich (1927) presented only two small quotes from field notes regarding bear predation, while Barnaby (1944) did not mention the subject. Other items of interest presented in Table 10-1 were that bears often ate only parts of the salmon, that they created distinct trails along the streams, that they were more numerous during the war years, and that the impact of bear predation varied with the size of the escapement. Finally, although many early visitors to the Karluk system saw the remains of salmon killed by bears, Hubbs (1941) nevertheless stated that "most intelligent observers do not regard the kill of salmon by bears as of any material significance." This may explain why Gilbert and Rich (1927) and Barnaby (1944) did not dwell on the matter.

[1] Troyer, Willard A., and Richard J. Hensel. ca. 1967. The brown bear of Kodiak Island. U.S. Bureau of Sport Fisheries and Wildlife, Branch of Wildlife Refuges, Kodiak. Unpubl. rep. 233 p. Located at ARLIS, Anchorage, AK.

Table 10-1

Anecdotal references of brown bear predation on sockeye salmon, Karluk River system, 1889–1946.

Observer	Date of observation	Location	Observation
Bean (1889: 368)	19 August 1889	South end of Karluk Lake	"... Goolia's sharp eye discovered a grizzly[1] with two cubs crunching salmon[2] ...."
Bean (1891: 198)	15–21 Aug 1889	Karluk Lake	"Bears consume large quantities of the breeding fish. They may be seen standing at the edge of the stream, where the water is shallow, and occasionally striking salmon with their claws and throwing them on the shore, where they are eaten alive."
Gilbert and Rich (1927: 13)	9 August 1921	Tent Point Creek	"Photos taken of fish off mouth and of fish partly eaten by bears a short distance upstream, where grass was trampled and evidence unmistakable of their presence ... "
Gilbert[3]	20 August 1922	Tributary of Thumb Lake	"... with these short and otherwise favorable streams, the greater part of the spawners must fall a prey to the bears."
Smith[4]	13 July 1928	Gull Creek	"As was the case last season the bear had taken a very heavy toll."
Smith[4]	13 July 1928	Canyon Creek	"The trail along the river is well marked by the ages of bear travel to and from the spawning area below the falls."
Smith[4]	3 Sep 1928	Upper Thumb River	"Because of the scarcity of fish the bear seem to be bedding down close to the river bank to take advantage of any opportunity to obtain their food, the salmon."
Hubbs (1941: 161)	1939	Alaska	"Some think that the bears destroy more salmon in Alaska than do any of the birds, but most intelligent observers do not regard the kill of salmon by bears as of any material significance."
Shuman[5]	10 July 1943	Salmon Creek	"Loss of fish to bears apparently enormous, though no estimate in numbers possible. Remains of those killed by bear are everywhere."
Shuman[5]	17 July 1943	Thumb Lake shore and tributaries	"The loss of fish to bear must be extremely high on these streams... it was estimated that fully 50% of the living fish ... bore marks ... made by bears claws (rarely by teeth)."
FWS[6]	1943	Karluk Lake	"Bear populations appeared to be greater than in any known previous year. (Probably due to lack of hunters, war activities on other portions of the island and a natural high survival of bears during the recent mild winters.) Estimated loss of spawning population (sockeyes) to bear; somewhere between 25% and 33%... Many small streams... had almost no spawning, all fish being taken by bear."
FWS[7]	1944	Karluk Lake	"Bears populations: appeared to be greater than in 1943.... Charlie Madsen (guide in Kodiak) placed the bear population in the Karluk basin at 500.... No hunters have been at the lake since 1941...A few of the smaller streams slightly (if at all) seeded, as bear killed all fish entering these streams. Bear should be decimated."
FWS[8]	July 1945	Karluk Lake	"On several of the smaller streams it was found that the bear were destroying every salmon entering to spawn, the seeding of the gravels thus remaining zero."
FWS[9]	1945	Karluk Lake	"An estimated 33% of entire escapement eaten or destroyed by bear."
Rich[10]	1945	Karluk Lake	"... one unexpected result of the war has been to drive much of the Kodiak Island population of *Ursus middendorfi* into the interior. They appear to be concentrated in the area around Karluk Lake... and there is no doubt that they could significantly reduce the numbers of spawning fish."
FWS[11]	1946	Karluk Lake	"Bears perhaps not as numerous this year as previous three years. However their depredations were found evident on all streams."

[1] Brown and grizzly bears are now considered to be the same species (*Ursus arctos*), and most people use "brown bear" when referring to that species near the Alaskan coast and "grizzly" when referring to that species in the Alaskan interior.

[2] In the Karluk River system the terms "salmon" or "fish" usually refer to sockeye salmon because that is the species of most interest.

[3] Gilbert, Charles H. 1922 notebook. Original notebook at Stanford University Libraries, Department of Special Collection and University Archives, Palo Alto, CA; typed summary of Gilbert's survey of Karluk Lake, 18–24 August 1922 located at NARA, Anchorage, AK.

[4] Smith, Seymour P. 1928 notebook. Original notebook location unknown; copies located at NARA, Anchorage, AK.

[5] Shuman, Richard F. 1943 notebook. Located at NARA, Anchorage, AK.

[6] Fish and Wildlife Service. 1943. Karluk weir, 1943 (Portage Trail Site). Unpubl. report. 1 p. Located at NARA, Anchorage, AK.

[7] Fish and Wildlife Service. 1944. Karluk weir, 1944 (Portage Trail Site). Unpubl. report. 1 p. Located at NARA, Anchorage, AK.

[8] Fish and Wildlife Service. 1943–52. Monthly Reports of the Alaska Fishery Investigations. Unpubl. reports. Located at NARA, Anchorage, AK.

[9] Fish and Wildlife Service. 1945. Karluk weir, 1945 (Outlet of Lake). Unpubl. report. 1 p. Located at NARA, Anchorage, AK.

[10] Letter (11 May 1946) from Willis H. Rich, Consultant, Salmon Fishery Investigations, to Elmer Higgins, Chief, Division of Fishery Biology, FWS, Washington, DC. Located at NARA, Anchorage, AK.

[11] Fish and Wildlife Service. 1946. Karluk weir, 1946 (Outlet of Lake). Unpubl. report. 1 p. Located at NARA, Anchorage, AK.

Investigations of Bear Predation at the Karluk River System from 1947 to Present

With a study on Moraine Creek in 1947, Shuman (1950) initiated the investigative approach to the bear predation on sockeye salmon question. The basis of the investigation was that a weir was installed near the mouth of Moraine Creek, a lateral tributary near the outlet of Karluk Lake (Fig. 1-5). Adult sockeye salmon were counted into the stream for an extended period each morning and evening. During the height of the run salmon were enumerated throughout the day. Dead fish which drifted downstream onto the weir were examined to determine cause of death (bear-killed or natural) and whether or not they had spawned at the time of death. When an examination of the gonads showed a fish to have completed less than one-half its spawning function, that fish was recorded as unspawned; when more than half had been completed it was recorded as spawned out. Sex was not determined for fish in the escapement or for carcasses that drifted onto the weir.

Results of the study were published in the Journal of Wildlife Management (Shuman, 1950) and are summarized here. Of a total of 14,826 sockeye salmon entering Moraine Creek, 5,393 later drifted back dead against the weir and 71.2% of that sample had been killed by bears; most importantly, 31.3% of the sample was killed unspawned (Table 10-2). Shuman attributed the high predation rate to a large number of bears in the Karluk Lake area due to a lack of hunting during the war years, the migration of bears away from military installations near the city of Kodiak, and a concomitant low sockeye salmon escapement. Shuman then made an extrapolation. Assuming that Moraine Creek was representative of all Karluk Lake spawning streams and after calculating the number of fish available to bear in the entire Karluk system to be 300,699, he multiplied that figure by 31.3%. The product was an unspawned bear kill of 94,119. If those salmon had been added to the commercial pack, he determined that they would have been worth $117,649. After deducting $9,000 for the value of bears shot in the Karluk Lake area, the net loss to bear predation was $108,649. On the basis of that information, Shuman urged immediate control of the bear population.

There were weaknesses in Shuman's paper, the most important of which was the extrapolation from data obtained for one year on one creek to the entire Karluk system, excluding the lake margins. Sockeye salmon spawned in many types of streams including lateral streams such as Moraine Creek, terminal streams such as O'Malley and Thumb rivers and Canyon Creek, and the upper 5 km of the Karluk River. The topography of these streams was vastly different. The lateral streams were shallower, faster, narrower, and shorter than the terminal streams and the upper Karluk River. Bears would have found catching a salmon much easier in a lateral stream like Moraine Creek than in the other stream types. Because the Karluk Lake spawning streams were so diverse, no single stream was representative of the entire system. Additionally, the monetary value of the salmon lost to bear predation was based on a number of questionable assumptions. For example, what assurance was there that every salmon that did not end up in the belly of a bear would have ended up in a can? Finally, the weir prevented the salmon from

Brown bear chasing sockeye salmon, Meadow Creek, Karluk Lake, 1966. (Benson Drucker, Reston, VA)

Table 10-2
Studies of brown bear predation on sockeye salmon using the carcass recovery method, Karluk Lake

				Dead fish examined on the spawning ground					
						Bear-killed sockeye			
							% of sample unspawned at:		
Investigator	Study year	Creek	Escapement to creek	Number	Percent of escapement	Percent of spawning ground sample	Weir	Stream and bank	Weir, stream, and bank
Shuman (1950)	1947	Moraine	14,826	5,393	36.4	71.2	31.3	—	—
Nelson et al. (1963)	1948	Moraine	61,160	18,484	30.2	55.5	26.3	—	—
Nelson et al. (1963)	1948	Halfway	10,230	6,757	66.1	37.3	9.6	12.6	11.1
Clark (1959)	1952	Moraine[1]	10,962	1,472	13.4	73.5	—	—	20.4
Clark (1959)	1952	Moraine[2]	10,962	9,407	85.8	2.5	—	—	0.6
Grogan (1969)	1953	Halfway[2]	2,148[3]	3,437	—	3.7	—	—	1.5
Clark (1965)	1955	Halfway[2]	2,845	2,147	75.5	25.5	0.7	3.3	1.5
Clark (1959)	1956	Halfway[2]	665	526	79.1	66.0	—	—	13.0
Gard (1971)	1964	Grassy Point	9,470	7,583	80.1	74.4	—	—	9.6[5]
Gard (1971)	1965	Grassy Point[2]	6,692	5,772	86.3	20.8	—	—	3.1[5]
Drucker[4]	1967	Grassy Point	1,395[5]	761[5]	54.6[5]	11.8[5]	—	—	1.1[5]
Drucker[4]	1967	Halfway	5,096[5]	2,659[5]	52.5[5]	20.0[5]	—	—	4.9[5]
Drucker[4]	1968	Grassy Point	4,080	2,771	67.9	93.8	—	—	11.2[5]

[1] Area above electric fence.
[2] All or part of area within electric fence.
[3] Partial escapement count due to defective weir.
[4] Drucker, Benson. 1973. Determining the effect of bear predation on spawning sockeye salmon on the basis of rate of disappearance of tagged salmon. BCF, ABL, Auke Bay. Unpubl. report. 46 p. Copy in the personal papers of Richard Gard, Juneau, AK.
[5] Females only.

returning to the lake which they would have done in an unbarricaded stream every afternoon or whenever a bear entered the stream. Because the salmon were held captive, bears could have caught them more easily with the result that the predation rate would have been higher than in an open stream. Despite these weaknesses, Shuman provided a valuable service to science by his study. He pioneered the investigative approach to understanding the question of bear predation on salmon and he stimulated several subsequent studies, all of which utilized weirs.

Shuman's paper proved to be controversial and the political implications were considerable. The sequence of events was as follows: Shuman prepared the manuscript during the winter of 1947–48 and submitted it to the FWS Washington office on 12 January 1948. Following a revision, official permission to publish was received from Washington on 3 May 1948. Perhaps this permission had been granted without a thorough review because Clarence Rhode, FWS Regional Director, Juneau, wrote the following letter to Albert Day, FWS Director, Washington, DC:

> When this report first came to my attention it had been cleared for publication and I felt then, as now, that it did not receive proper routing in the Central Office. This, however, is certainly no fault of Mr. Shuman's. . . [2]

In any event, from the revised edition mimeographed copies were prepared by the FWS Regional Office in Juneau and released on 4 February 1949. Some of these copies found their way to the Alaska Territorial Legislature, which was then in session. Partly because of Shuman's study, the Alaska House of Representatives on 16 February 1949 passed Memorial No. 3 which urged the removal of the limit on brown bears. Alaska was a Territory at that time and actions taken by the Territorial Legislature were only recommendations to be considered by a branch of the federal government, in this case the U.S. Department of the Interior. Apparently House Memorial No. 3 was not viewed favorably by the Secretary of the Interior because the limit on brown bears was kept the same as before – one bear on Kodiak Island.

The next meeting of the Alaska Territorial Legislature was in 1951 and Shuman's paper was again a subject of debate. Following a proposal by the Kodiak Island

[2] Letter (ca. July 1951) from Clarence J. Rhode, Regional Director, Juneau, AK, to Director, Washington, DC. Located at NARA, Anchorage, AK.

Bear-killed sockeye salmon, Karluk Lake, July 1948. (Auke Bay Laboratory, Auke Bay, AK)

cattlemen to have the season and limit on bears removed (bears do kill some cattle) and a rebuttal by hunting guides and the FWS, came a summary of Shuman's findings. This was the same information that was presented in the 1949 legislative session, the only difference being that the results had now been formally published (Shuman, 1950). There was a second rebuttal, but when it came to a vote, the House and Senate passed Joint House Memorial No. 6 which urged that the season and bag limit on bears be removed. Curiously, although Shuman's work was presented during the debate, it was not mentioned in the Memorial itself as it was in 1949. As was the case with the 1949 Memorial, the 1951 Memorial was not supported by the Secretary of the Interior.

A third political event involving Shuman's paper was initiated in June 1951 when Frank Dufresne published an article in *Field and Stream* magazine (Dufresne, 1951). Dufresne apparently was trying to cause a split in the FWS into a commercial fisheries group and a sport fish and wildlife group because he thought they had different missions and should be separated. He accused Shuman of causing dissension in the FWS by publishing material that was contradictory to the official FWS policy concerning bear control. Both Shuman[3] and Clarence Rhode denied this accusation:

> [Discussing Shuman's 1950 paper] I hate to think that the sportsmen of America will join hands with the salmon packers to split the fisheries from wildlife, but that could be one result of this article. Frank [Dufresne] was looking for something "hot" and this was the only thing he could find that apparently suited his purpose. . . . we are infinitely better off as a unified Service than would be the case if these two operations were divided.

Nevertheless, the commercial fisheries and wildlife programs were officially separated on 1 July 1955 and these two groups later became known as the U.S. Bureau of Commercial Fisheries and the U.S. Bureau of Sport Fisheries and Wildlife. Whether or not Shuman's or Dufresne's report had anything to do with this split is moot.

Following Shuman's 1947 Moraine Creek study were several subsequent bear predation on sockeye investigations at Karluk Lake (Table 10-2), which we describe below.

Moraine and Halfway Creeks: 1948

Shuman and Nelson conducted a second study of bear predation at Karluk Lake in 1948. Observations on Moraine Creek were made in essentially the same manner as in 1947. However, at Halfway Creek, another lateral stream of Karluk Lake, the sample of fish examined included not only carcasses that floated onto the weir, but also carcasses in the stream and on the stream banks. This latter group of carcasses was examined and removed from the area every five days.

The first manuscript summarizing the 1948 data was written by Shuman and Nelson in 1950. Like Shuman's 1950 paper, this report also had a stormy history because the FWS did not want a replay of the problems generated by the earlier paper. Many revisions were required and other authors and studies became involved, as did both FWS branches.

In 1954 Shuman died in an airplane accident, and Nelson assumed senior authorship and transferred to

[3] 1) Letter (20 June 1951) from R. F. Shuman, Fishery Management Supervisor, FWS, Juneau, AK, to Regional Director, FWS, Juneau, AK.
2) Letter (12 July 1951) from R. F. Shuman, Fishery Management Supervisor, FWS, Juneau, AK, to Regional Director, FWS, Juneau, AK. Both located at NARA, Anchorage, AK.

Washington, DC. Administrations changed and at least 50 letters and memoranda were exchanged concerning the study. Finally, in 1961 an acceptable manuscript was produced ("Brown bear predation on spawning salmon, 1948–1953, Kodiak Island, Alaska") and authored by Nelson, Shuman, Clark, and Hoffman. The manuscript was issued as a Manuscript Report of the Auke Bay Laboratory Library in 1963. Important information in the manuscript included the findings that 26.3% and 11% of the carcasses examined at Moraine Creek and Halfway Creek, respectively, were unspawned and bear-killed (Table 10-2). Also included were data from other Kodiak Island streams and a discussion of experimental errors.

Moraine Creek: 1952

In 1952, FWS Kodiak National Wildlife Refuge personnel conducted a third bear predation study on Moraine Creek to determine if the installation of an electric fence around part of the creek would reduce bear predation on sockeye salmon (Clark, 1959). Methods were the same as in earlier years, except that an electric fence was installed around the lower four-fifths of the spawning area, dead fish in the stream and along the stream banks were enumerated, and a second weir was constructed at the upper end of the fence. This upper weir was designed to catch most dead fish that drifted from the spawning area above while permitting live fish to pass in either direction. Results were that above the fence 73.5% of the sample were bear-killed whereas within the electric fence only 2.5% were bear-killed (Table 10-2). Percentages of unspawned bear-killed fish above and within the fence were 20.4% and 0.6%, respectively. Clearly, bear predation on salmon within the fenced area was greatly reduced.

Halfway Creek: 1953

A somewhat different type of bear predation investigation was conducted by FWS Kodiak National Wildlife Refuge personnel on Halfway Creek in 1953 (Grogan, 1969). Near the mouth of the creek, a small island divided the creek into two parts. This permitted the installation of a weir on one side of the island and an escape pond on the other side. The escape pond extended into the lake where a fence prevented sockeye salmon from returning to the main body of the lake. The purpose of the pond was to create a relatively deep, safe haven into which spawning salmon in the stream could flee to escape a pursuing bear. Both pond and weir were surrounded by an electric fence. Once each day fish were counted through the weir and carcasses were collected from the weir face and from the escape pond, assessed as in 1948, and removed from the stream bank. Every seven days, all dead fish in the stream and on the stream banks were examined and removed from the area.

Bear predation was minimal as only 1.5% of the carcasses examined were killed unspawned by bears (Table 10-2). Although the bear population in the Karluk Lake basin was about the same as in 1952, bears apparently did not feed on salmon in the Karluk tributaries as heavily as in earlier years. Grogan (1969) attributed this to an early, bumper crop of elderberries, *Sambucus recemosus pubens*. When elderberries were available, bears preferred these to sockeye salmon. Elderberries apparently had flourished because of a warm, dry spring and early summer.

Halfway Creek: 1955

Design of the 1955 investigation was similar to that employed in 1953 except that a sample of sockeye salmon was seined and tagged at the mouth of the stream and their spawning status was checked daily by dip-netting them at their spawning location (Clark, 1965). Results were that 25% of the carcasses examined had been killed by bears, but the bear take of unspawned fish was only 1.5%, the same as in 1953 (Table 10-2). Bears appeared on the stream late in the season, probably the result of a late-ripening elderberry crop, which kept them browsing on the slopes later than usual. The tagging experiment indicated that: 1) both sexes of sockeye salmon remained in the lake off the stream mouth until they became ripe, 2) after they entered the stream, spawning started immediately, 3) within 24 hours a female may have deposited 50% or more of its eggs, 4) netting of fish was difficult when they were fresh, but became easier after spawning was completed, and 5) they returned to the safety of the lake when molested by bears or humans. Because of these behavioral traits Clark (1965) concluded that bears have little chance to take wholly unspawned salmon in small streams.

Halfway Creek: 1956

Methods in 1956 were the same as those used in 1955 (Clark, 1959). Total bear-take of the sockeye salmon sample was 66.0% and unspawned bear-take was 13.0% (Table 10-2). Both figures were the highest obtained during four years of study. Higher bear predation in 1956 was probably due to the lowest escapement on record (138,000 at Karluk River weir and 665 at Halfway Creek weir) and to the fact that several unspawned fish were caught by bears in the escape pen before the electric fence was installed. It appeared that the escape pen was ineffective in 1956.

Bear-killed sockeye salmon, Karluk Lake tributary, 1965. (Benson Drucker, Reston, VA)

Grassy Point Creek: 1964 and 1965

Data for 1964 and 1965 are treated together because they constitute one study. In 1964 Grassy Point Creek, a lateral stream, was unfenced while in 1965 it was completely surrounded by an electric fence. Gard (1971) conducted this investigation following methods used in earlier studies described by Clark (1959) with the differences noted below. The sex of the sockeye salmon escapement and of the sample of carcasses was determined. Carcasses were collected from the weir, stream, and stream banks twice each day and were deposited in the lake after they were examined for spawning status. Spawning status was determined for intact female carcasses only; eggs were counted in individuals of questionable status. In 1964 a downstream escape pen designed to enable salmon to evade bears was attached to the weir, but it was removed because bears tore off the cover and killed the trapped salmon. Three lots of 100 fish each were tagged at the weir (1964 only) and their longevity determined during twice-daily stream surveys. Loss of eggs to bear predation was calculated from potential egg deposition, actual egg deposition, and information collected at the weir and during the carcass assessments. (see Gard, 1971 for details).

Results of the investigation follow. Percentages of the sockeye salmon escapements examined on the spawning grounds were 80 in 1964 and 86 in 1965, the highest reported in any predation study (Table 10-2). High recoveries were probably due to more frequent stream cleanups than in earlier studies. Bears were efficient predators in Grassy Point Creek, killing up to 74% of the salmon in 1964; however, only 9.6% of a sample of bear-killed females were unspawned. The maximum estimate of sockeye salmon eggs lost to bear predation in 1964 was about 1,000,000 compared to a total loss from all causes of 8,000,000 potential eggs. The ratio of males to females in each year's escapement approached 1:1, whereas the ratio among bear kills was about 3:2. Thus, males acted as a buffer against predation of females. The electric fencing reduced bear predation by two-thirds in Grassy Point Creek.

Grassy Point and Halfway Creeks: 1966, 1967, 1968

This bear predation study by Benson Drucker[4] included the 1964 data and methods reported by Gard (1971), except that the streams were unfenced, salmon escapements into Grassy Point Creek in 1967 and 1968 were restricted, and eggs were counted in each female carcass found during the 1967–68 stream surveys. Additionally, Drucker calculated sockeye salmon mortality rates from the rate of disappearance of tagged spawners in 1964, 1966, and 1968 and attributed all mortality during spawning to bear predation. He then compared the mortality rates found by the two methods, using 1) carcass recovery and 2) rate of disappearance of tagged spawners.

Results were substantially different depending on the method used. In the carcass recovery method, unspawned, bear-killed female sockeye salmon ranged from 1.1% to 11.2% in Grassy Point and Halfway Creeks, which indicated low to moderate predation when compared to other studies (Table 10-2). However, in the disappearance of tagged spawners method, unspawned

[4] Drucker, Benson. 1973. Determining the effect of bear predation on spawning sockeye salmon on the basis of rate of disappearance of tagged salmon. BCF, ABL, Auke Bay. Unpubl. report. 46 p. Copy in the personal papers of Richard Gard, Juneau, AK.

bear-killed females ranged from 39% to 79% in Grassy Point Creek, with the highest predation rate occurring in 1968.

Another indicator of extreme predation in 1968 was that average number of eggs in the females examined was almost four times greater than in 1967. Presumably nearly constant harassment by bears interrupted the spawning act. Calculated number of eggs lost to bear predation for the entire stream in 1964 was 4 or 5 million depending on whether spawning was completed in 2 or 3 days, whereas Gard (1971) calculated eggs lost to bears in 1964 to be only 1 million by the carcass recovery method. In the 1968 carcass samples the ratio of females to males killed by bears was significantly higher at Halfway Creek than was expected from the sex ratio at the weir, but there was no difference at Grassy Point Creek. However, Gard (1971) found that bears selected males at Grassy Point Creek in 1964–65.

Drucker believed that the disappearance of tagged spawners method produced more realistic estimates of the effects of bear predation on sockeye salmon than did the carcass recovery method because eggs were often lost when a ripe female was struggling in the jaws of a bear. Such fish might have been classified as spawned out, but in reality were unspawned at the time of capture. This did happen in an unknown number of cases and the numbers of unspawned, bear-killed females determined from samples of carcasses may have been lower than they really were.

It was equally true that there were errors associated with the disappearance of tagged spawners method. Firstly, the assumption was made that all disappearances of tagged fish were due to bear predation. However, there were other reasons for tagged fish to disappear, including loss of tags, increased mortality caused by the presence of tags, and predation by other animals. Red foxes killed 1% of the carcasses inspected at Grassy Point Creek in 1965 (Gard, 1971). Also, bald eagles, river otters, and various species of gulls may have taken sockeye salmon. Clark (1965) found four sockeye salmon in six bald eagle nests he inspected, but did not comment on the spawning status. Secondly, the assumption was made that all salmon females required 2 or 3 days to establish a redd site and spawn. Because Clark (1965) and Owen[5] reported that many sockeye salmon females were spawned out after only 24 hours in Grassy Point and Cottonwood Creeks, respectively, the 2- or 3-day spawning periods assumed by Drucker were unrealistically long.

Summary and Conclusions

Many animals preyed on adult sockeye salmon in the Karluk River system, but the brown bear was easily the most important. Other predators included red foxes, river otters, bald eagles, and various species of gulls. None of these other predator species was by itself significant, but the total impact of all these species might have been appreciable. Information on these predators was scarce and largely anecdotal.

Perhaps the most significant information revealed by the bear predation on sockeye salmon studies was that predation rates varied greatly between lateral streams during one year or between years for one stream. For example, in unfenced streams there was about a 2-fold difference in bear-take of unspawned fish between streams in 1948 and 1968 and a 10-fold difference between 1967 and 1968 at Grassy Point Creek (Table 10-2). These results emphasize the fallacy of extrapolating from data collected from only one stream or year. Once again, the wide diversity of biological responses in space and time are evident for the Karluk Lake ecosystem.

The most important variable influencing the effect of bear predation probably was the size of the sockeye salmon population. During the years of study, sockeye salmon escapements to Karluk Lake varied greatly from 138,000 in 1956 to 754,000 in 1948, while estimates of the bear populations varied moderately from 115 in 1953 (Clark, 1959) to 156 in 1962.[6] In years with low escapements a relatively constant number of bears could have had a substantial effect on the sockeye salmon population, but in years of large escapements the effect of predation would have been insignificant or even beneficial. In 1947 there was a relatively small escapement to Moraine Creek of 14,826 fish and the unspawned bear-take was 31.3%, whereas in 1948 the escapement was 61,160 and the unspawned bear-take dropped to 26.3% (Table 10-2). Also in 1956 when the escapement to Halfway Creek was only 665 (the smallest on record) the unspawned bear-take was a relatively high 13.0%, whereas in 1955 with an escapement of 2,845 the unspawned bear-take was only 1.5%. Rounsefell (1958) demonstrated that the Karluk sockeye salmon reproduction curve was of the "Ricker type" and suggested

[5] Letter (13 July 1957) from John B. Owen, Fishery Research Biologist, to W. F. Royce, FWS, Juneau, AK. Located at NARA, Anchorage, AK.

[6] See footnote 1.

that when the escapement was large enough for the expected return to fall along the right limb of the curve, some bear predation could have increased the return.

During the peak of the spawning run sockeye salmon were often the preferred food of brown bears, but at other times bears ate a variety of plant foods. Elderberries were of special interest because bears apparently preferred them to salmon, even when the latter were readily available. In 1953 there was an abundant, early elderberry crop and bears left Halfway Creek early to feast on the berries, with the result that the bear-take of unspawned fish was only 1.5% (Grogan, 1969). Due to a late vegetative season in 1955, bears apparently grazed on the high slopes later in the summer than usual and stayed on to browse on the late-ripening elderberry crop (Clark, 1965). The result was that bears spent little time on Halfway Creek that year and the bear-take of unspawned fish was again only 1.5%. Berns et al. (1980) and Barnes (1990) also mentioned the importance of elderberries in the diet of brown bears during August and September.

Sockeye salmon have evolved several behavioral traits that permitted them to flourish in the shallow lateral streams of Karluk Lake despite bear predation. These behaviors included: 1) remaining in the lake until ripe, 2) quickly building a redd and spawning, often depositing over half their eggs within 24 hours following stream entry, and 3) returning to the safety of the lake each afternoon or if disturbed by bears.

Electric fences were installed around all or part of the three test streams to determine if they would reduce bear predation on sockeye. Percentages of unspawned bear-take in these streams were 0.6, 1.5 (twice), 3.1, and 13.0, with an average of 4.8. The 13% figure was for Halfway Creek in 1956 when the escapement was at an all time low. Comparable percentages for unfenced streams ranged from 1.1 to 31.3, with an average of 12.7 (Table 10-2). Therefore, electric fences usually restricted bear predation on sockeye salmon to very low levels and were the least damaging and least expensive method to protect sockeye salmon in small streams when escapements were low. However, regular fence maintenance was required during the spawning period because bears occasionally broke the fences to reach the streams.

There was no consistent pattern of differential predation by bears on male or female sockeye salmon. In 1964 and 1965 male sockeye salmon were selected by bears at Grassy Point Creek. In 1968 neither sex was selected at Grassy Point Creek, but females were selected at Halfway Creek. Therefore, there was no justification for permitting a differential harvest of either sex in the Karluk commercial fishery.

Escape pens were constructed at the stream mouths during four studies to provide safe havens to which spawning salmon could have retreated during bear harassment. In two studies the results were inconclusive because few bears visited the streams and in the other two studies bears got into the pens and probably killed more salmon than they would have had there been no pens.

In the opening paragraph of this chapter the question was posed as to whether or not control of brown bears, as was suggested by Shuman (1950) and the Alaska Territorial Legislature (1949, 1951), would result in an increased number of sockeye salmon. We may never know for certain the answer to that question when directed toward the situation existing at Karluk Lake in the 1940s and early 1950s because control measures were never put into effect. What we do know is that during the late 1940s sockeye salmon escapements were falling and that bear numbers were high due to lack of hunters and bear migrations during World War II. We also know that bear populations remained fairly steady after 1951 and that sockeye salmon escapements oscillated around 400,000 through 1984, but in recent years approached 1 million fish (Fig. 1-3). This resurgence came without any control of bears. Further, we know that most of the studies in the 1950s and 1960s found bear-take of unspawned fish to be low to moderate. Therefore, we conclude that bear predation usually has little effect on sockeye populations at Karluk Lake and that control of bears by means other than sport hunting would not be justified and, in fact, could be detrimental in years of high sockeye salmon escapements.

CHAPTER 11

Theories of Population Decline and Recovery

Everyone had a theory and the battle raged!

The sockeye salmon of the Karluk River declined in abundance between about 1890 and the early 1980s, followed by a recovery that began in about 1985 (Figs. 1-2, 1-3). The cause(s) of the long-term decline has been an ongoing scientific controversy during most of Karluk's fisheries history. Many prominent fishery biologists have proposed different theories to explain the persistent diminution of these salmon runs. The credence given to the growing array of theories changed over the years as different biologists studied the problem and conducted new research at Karluk. In this chapter, we discuss 12 plausible theories that have been proposed to explain the long-term decline and subsequent recovery of sockeye salmon abundance in the Karluk River. Because much of the sockeye salmon research conducted at Karluk over the past 100 years was a search for these root causes, this chapter, in effect, is a summary of this book.

Overfishing of the Entire Run, Especially in the Early Years

During the first 40 years (1882–1921) of commercial fishing of Karluk River sockeye salmon, more than 74,000,000 fish were harvested, averaging over 1,800,000 fish per year. During the 20 year peak period from 1888 to 1907, the commercial catch averaged over 2,600,000 fish per year from this one rather small river. These astonishing statistics document the enormous harvests made during the early years of the fishery. Federal inspectors and other visitors to Karluk in these early years often believed that the sockeye salmon were being over-harvested, but that was largely an intuitive response to seeing each seine haul bring ashore many thousands of fish from the small river, not based on actual data on the sustainable productivity of the system. Some cannery officials were also worried that the salmon runs might falter at Karluk, and the APA voluntarily built a sockeye salmon hatchery in 1896 to hopefully bolster future runs. Thus, overfishing of the entire run was the earliest and most persistent theory to explain the decline of Karluk's sockeye salmon, though the actual biological mechanism of how this occurred remained unclear for many years.

There are three biological mechanisms by which overfishing of the entire run might have led to the declining abundance of Karluk's sockeye salmon: 1) too few adult salmon were present to fully seed the spawning grounds at Karluk Lake, 2) too few adult salmon were present to transport important nutrients into Karluk Lake, and 3) juvenile sockeye salmon had poor survival in Karluk Lake because fry emergence and plankton blooms were not synchronized. The initial concerns about overfishing were focused entirely on the first mechanism of spawning sufficiency, and these worries already were obvious within 6–8 years after the fishery started in 1882. Yet, remarkably, prior to 1926 no one considered the impact that overfishing might have on the nutrient levels in Karluk Lake and on the ability of the lake to rear juvenile sockeye salmon. In this section we briefly discuss the first mechanism, spawning sufficiency, and the following two mechanisms will be considered in subsequent sections.

The overfishing theory was based on the heavy exploitation of Karluk's sockeye salmon and the assumption that the numbers of returning salmon were directly proportional to brood-year escapements. However, the validity of this theory was questioned after Barnaby (1944) and Rounsefell (1958) demonstrated that returns were not proportional to escapements. The theory was questioned further when sockeye salmon runs failed to recover after implementation of the 1924 White Act, which mandated that at least 50% of the total run must be allowed to escape the fishery. Fifty percent escapement was considered to be a generous proportion that certainly would guarantee full seeding of the spawning grounds at Karluk Lake. Once the Karluk River weir began operating in 1921, mangers

monitored the seasonal progression of harvests and escapements to assure compliance with the White Act, but still the runs continued to decline.

During the early fishery (1882–1920), there was no direct measure of sockeye salmon escapement to the spawning grounds and very little interest in whether they were fully-seeded or under-seeded. The few biologists who did visit Karluk Lake in these years seemed to be impressed with the numbers of spawning sockeye, suggesting that seeding may have been adequate. The only accurate counts of spawning fish during this era were those made by Rutter in August 1903, when he tallied nearly 22,000 adult sockeye salmon in Moraine Creek, a number suggesting full seeding. Once the weir program began in 1921, sockeye escapements to the spawning grounds were accurately measured. Eventually, biologists measured the actual spawning areas to learn just how many spawners could be accommodated in the Karluk system; the estimate ranged between about 500,000 and 1,000,000 fish. During 1921–38, sockeye salmon escapements at Karluk averaged about 1,100,000 fish, a number that should have fully seeded the spawning grounds (Fig. 1-3). Yet, despite relatively large escapements, the decline of Karluk's sockeye salmon continued unabated from 1939 to 1984. Thus, it appears that most of the long-term decline in Karluk's sockeye salmon was not caused by under-seeding of the spawning grounds, though some of the extremely low escapements during 1954–82 may have been inadequate.

Reduction of Lake Fertility

The lake fertility theory asserted that the continual large harvests of sockeye salmon by the commercial fishery reduced the number of fish that reached Karluk Lake and thereby decreased the nutrients that were annually added to the lake when the adult salmon died and their carcasses decomposed (Juday et al., 1932; Barnaby, 1944; Nelson and Edmondson, 1955). Smaller nutrient influxes (especially of nitrogen and phosphorus) would reduce phytoplankton and zooplankton production, which in turn would decrease the growth of juvenile sockeye. Macrozooplankton were the main food of these young fishes at Karluk Lake. This chain of events would lead to smaller smolts that had lower survival rates in the ocean and fewer adults that returned to the Karluk system. The theory of reduced lake fertility is a direct consequence of overfishing and is not thought to be an independent natural phenomenon within the Karluk River drainage basin.

Willis Rich was the first to suggest in 1926 that salmon-carcass nutrients might be important to the productivity of Karluk Lake.[1] In 1935–36 Barnaby (1944) found less soluble phosphorus and silica in the surface waters of Karluk Lake than had been present in 1927 (Juday et al., 1932); however, the phosphorus levels in 1958 were reported to be similar to those in 1927 and silica contents were higher (Conkle et al., 1959). Since sockeye salmon escapement was 873,000 in 1927, but only 219,000 in 1958, it was concluded that lake nutrients were independent of the number of salmon carcasses. Yet, limnological studies in the late 1970s and early 1980s demonstrated large seasonal variations in the phosphorus content of lake waters, with considerable declines in this nutrient between 1927 and the 1980s (Koenings amd Burkett, 1987b). Significantly, these studies showed that the annual influx of phosphorus to the lake from salmon carcasses was equal to or greater than that derived from watershed runoff. Hence, salmon-carcass nutrients were important to the productivity of juvenile sockeye salmon in Karluk Lake.

Barnaby (1944) concluded that juvenile sockeye must rear an extra year in Karluk Lake because diminished food supplies reduced their growth rates. In contrast, Rounsefell (1958) claimed that there had been no decrease in the lake's food supply since a strong linear relationship existed between smolt numbers and biomass, and he found no significant decrease in the size of similar-aged smolts over the years. Rounsefell's results on sockeye smolts, however, were not supported when a longer time period was examined. Smolt size had decreased for all age groups during 1922–84, strongly suggesting that Karluk Lake's fertility had declined (Koenings and Burkett, 1987a).

Nelson studied the effect of lake fertility on plankton production and growth of young sockeye salmon at Bare Lake. When he added commercial fertilizers to the lake during 1950–56, phytoplankton production and juvenile sockeye growth increased (Nelson and Edmondson, 1955; Nelson, 1959). Although some questions existed about whether the Bare Lake fertilization results could be applied to the much larger Karluk Lake, it appeared that its juvenile sockeye would also benefit from fertilization. The ADFG fertilized the main basin of Karluk Lake during 1986–90 to increase its productivity and rehabilitate its sockeye salmon runs. Larger escapements of sock-

[1] Rich, Willis H. 1926 notebook. Location of original notebook unknown; copies at NARA, Anchorage, AK, and ABL Library, Auke Bay, AK.

eye entered Karluk Lake during the fertilization years and added to its fertility.

Although the fertility theory is based on the continual loss of sockeye salmon nutrients to Karluk Lake, pink salmon also occasionally transport additional carcass nutrients to the lake. Pink salmon typically spawn in the Karluk River below the lake, but when their escapements exceed 1,500,000–2,000,000, they enter Karluk Lake and spawn in its tributary streams. Because of their smaller body size and irregularity in reaching the lake, nutrient contributions from pink salmon carcasses have a smaller, but still positive, impact on lake fertility. This phenomenon illustrates another complexity in the life cycle of Karluk's sockeye salmon—nutrient linkages between parents and offspring, between several year classes, between spring and fall runs, and between sockeye and pink salmon.

Considerable evidence has accumulated over the years that lake fertility is important to the survival and production of sockeye salmon at Karluk. We believe that the lake fertility theory is an important part of a broader hypothesis (see ocean climate–lake fertility theory) for understanding the long-term decline of Karluk's sockeye salmon. Yet even when considered alone, the lake fertility theory provides an explanation for the long-term decline that began soon after commercial fishing commenced in 1882.

Asynchrony Between Plankton Blooms and Fry Emergence at Karluk Lake

This theory asserted that the sockeye salmon runs at Karluk were damaged because a mismatch existed between the timing of plankton blooms and arrival of newly emerged fry to the lake. Foerster (1968), Di Costanzo,[2] and Koenings and Burkett (1987b) have discussed the heavy mortality that would occur if young sockeye that had just migrated to their nursery lake were unable to find an adequate food supply of macrozooplankton.

Because of the many subpopulations of sockeye salmon at Karluk, newly emerged fry reach the lake over a wide temporal range. Fry from spring-run spawners enter the lake in April and May, with a few arriving as late as mid-June (Gard and Drucker, 1965). Next, the fry from Thumb and O'Malley lakes and the first wave from the upper Karluk River arrive in May and early-June (Burgner et al., 1969).[3] Finally, the progeny of fall spawners, including the second wave from the upper Karluk River, arrive at the lake in late June, July and August (Gard and Drucker, 1965).[4]

For many years, it was thought that feeding conditions for sockeye fry were optimal in the spring, after water temperatures rose and the plankton bloomed in late-May (Hartman et al., 1967). In this scenario, the progeny of spring-run sockeye reached the lake at a propitious time (April and May) to feed on the plankton bloom, while the progeny of fall-run spawners arrived too late for optimal feeding and suffered increased mortality. However, more recent research has documented that a second plankton bloom (Fig. 4-10), which is much larger than the spring bloom, occurs at Karluk Lake from late-August to November (Hilliard, 1959a; Koenings and Burkett, 1987b; Schmidt et al., 1998). As a result, it now appears that early emerging fry were out of synchrony with the major food supply. Though late-emerging fry had less time to feed before they entered their first winter, they may still have prospered because of the abundant food supply.

How did this asynchrony of fry emergence and food supply come about? Koenings and Burkett (1987b) hypothesized that formerly there were many sockeye salmon age groups (24 by latest count) and that some of these, now depleted by overfishing, spawned in the midseason. Offspring of midseason fish would have emerged at a time intermediate to early and late emerging fry. That is, midseason fry would have emerged late enough to avoid the cold temperatures of early spring, but early enough to benefit from a full season of feeding on macrozooplankton before the onset of winter. Since June was the only time during their study when few fry emerged, this seemed to be when offspring of the supposedly abundant mid-season spawners had once emerged.

The solution proposed by Koenings and Burkett (1987b) to restore the synchrony of fry emergences and plankton blooms was two-fold. First, they recommended that Karluk Lake be fertilized at a time to enhance the plankton forage of the critical spring period, but they failed to specify when that time might have been. It ap-

[2] DiCostanzo, Charles J. 1972. Comments by Charles J. DiCostanzo on the manuscript: "Evaluation of causes for the decline of the Karluk sockeye and recommendations for rehabilitation" by Drs. R. Van Cleve and D. E. Bevan. NMFS, ABL, Auke Bay, Alaska. Unpubl. report. 39 p. Located at ABL Office Files, Auke Bay, AK.

[3] Walker, Charles E. 1954. Karluk young fish study, 1950–1954. Kodiak Island Research, FRI, University of Washington, Seattle. Unpubl. report. Located at FRI Archives, University of Washington, Seattle, WA.

[4] See footnote 3.

peared that all stocks and ages of juvenile sockeye would benefit from the fertilization, regardless of the time of application. Second, since spring-run sockeye required more spawners to compensate for the disadvantages of early fry emergence, they recommended lower harvests of spring-run fish and a gradual increase of harvest into fall. They also suggested that eyed sockeye salmon eggs should be planted in the Upper Thumb River, which historically had a large spring run.

The response to their recommendations was mixed. Karluk Lake was fertilized between 1986 and 1990, but the eyed egg plants in Upper Thumb River were terminated in 1986 and the progressive low to high harvest rate strategy was not employed (Prokopowich et al., 1998; ADFG, 1998). During the 1990s the runs of sockeye salmon increased at Karluk, but not to the previous high levels experienced during the early fishery. Furthermore, it was not entirely clear that the lake fertilization project was solely responsible for the larger runs because sockeye salmon returns began to increase in 1984 or 1985, before the enrichment program began. And unexpectedly, sockeye salmon runs increased in many river systems around Kodiak Island during this period, even though most had not been fertilized.

The asynchrony theory is difficult to evaluate because the lake fertilization and eyed egg plants may not have been carried out long enough to produce lasting results, and the harvest strategy recommended by Koenings and Burkett (1987b) was not followed. It remains a plausible, though complex, hypothesis to explain the decline of Karluk's sockeye salmon. Its complexity comes from the multiple factors that influence plankton blooms in the lake—seasonal insolation, water temperature, stored nutrients, salmon-carcass nutrients, watershed nutrients, fish predation, and sockeye salmon escapements—and from the many different sockeye subpopulations and age classes that rely on and benefit from the planktonic forage base.

Overfishing of Productive Midseason Subpopulations

The midseason subpopulation theory claimed that the long-term decline of Karluk's sockeye salmon occurred because the early fishery was heavily concentrated on midseason fish, which ostensibly were the most productive and abundant group of the entire run. Loss of the abundant midseason subpopulations reduced the entire run and changed the original run distribution from unimodal to bimodal. This theory has been discussed and investigated by Thompson (1950), Owen et al. (1962), and Gard and Drucker (1986) and was supported by many fisheries biologists from about 1960 to 1990. Indeed, Burgner (1991) stated that "It is commonly accepted that overfishing of productive midseason sub-populations was largely the cause of the initial decline of Karluk River sockeye ..." This theory is consistent with the increased freshwater mortality since 1928 that Rounsefell reported (1958). That is, depletion (or possibly extinction) of one or more midseason spawning units that once had low mortality in freshwater would increase the total freshwater mortality for the system.

The midseason subpopulation theory is based upon four natural and historical features of Karluk's sockeye salmon: 1) the existence of subpopulations (see Chapter 5), 2) the seasonal run distribution (see Chapter 6), 3) the increase in relative fecundity (Fig. 4-8), and 4) the heavy exploitation of midseason fish by the commercial fishery. The midseason subpopulations of sockeye salmon were heavily harvested in the early Karluk fishery; weekly harvest rates from 5 July to 16 August in 1922–1936 averaged 68% (Fig. 11-1). To help reestablish these subpopulations, partial midseason closures were enforced on the fishery from the mid 1950s to 1975, and the midseason harvest rates averaged 44% during the 1962–75 period. Nevertheless, despite 20 years of decreased harvest rates, the midseason runs failed to significantly increase (Fig. 6-2). It is unclear why these reportedly productive groups never responded to protection from the fishery—either the groups had been totally eliminated or possibly they were not as productive as previously believed. Our review of the historical literature (Chapter 6) suggests that the original run distribution of Karluk's sockeye salmon was bimodal, not unimodal, and that midseason subpopulations were not the most abundant and productive group. Thus, while the midseason subpopulation theory appears to retain some plausibility, we believe that it was not the main cause for the long-term decline in Karluk's sockeye salmon and certainly cannot be given credit for the more recent recovery since 1985.

Changes in the Physical Environment of the Spawning Habitat

This theory claimed that sockeye salmon abundance declined because something in the local physical environment at Karluk changed. It is difficult, however, to find any long-term changes in the nearly pristine environment of Karluk Lake and River. For example, since 1869 no detectable changes in temperature or precipitation have been recorded at the town of Kodiak, a re-

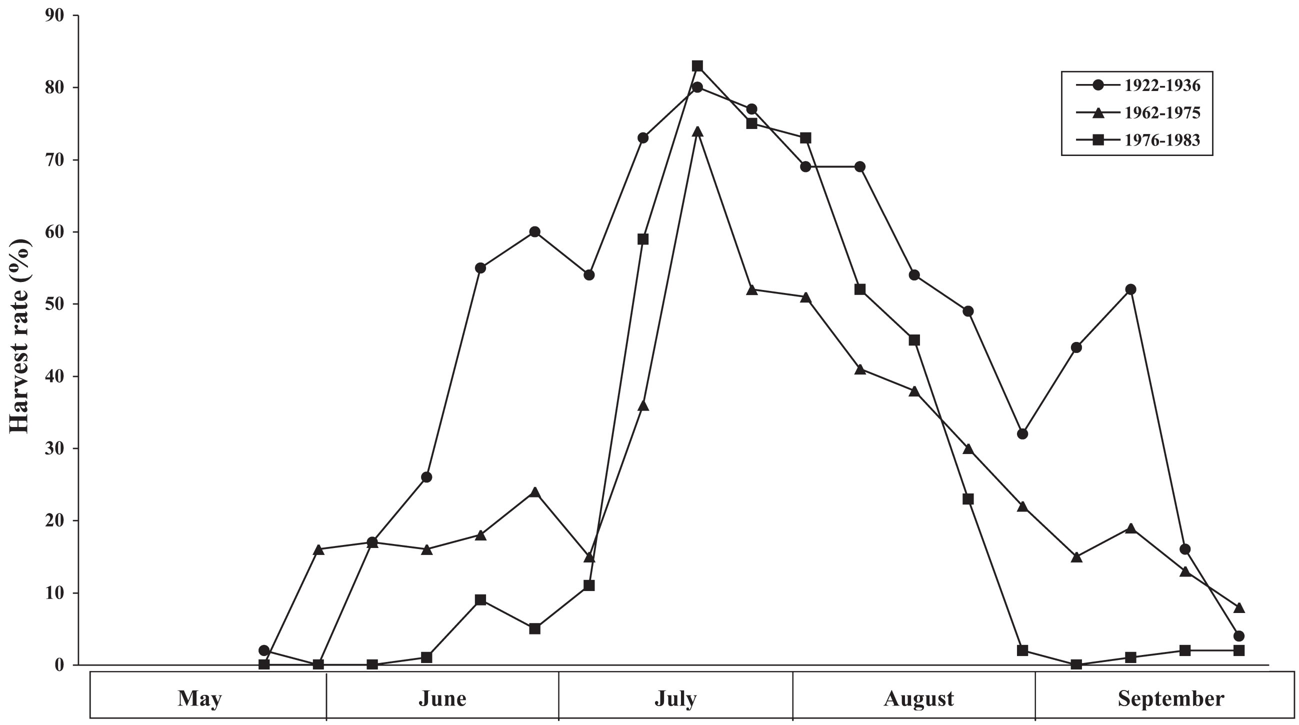


Figure 11-1. Harvest rates for Karluk River sockeye salmon, 1922–83.

sult that probably also applies to the Karluk River system (Rounsefell, 1958). Likewise, no important changes have occurred in the land-use, pollution, and human populations of the Karluk River watershed.

It is undoubtedly true that the Karluk system occasionally was affected in past eons by ash falls from volcanic eruptions on the Alaska Peninsula (Eichler and Rounsefell, 1957). Ample evidence of ash falls has been found in sediment layers exposed in archaeological excavations and sediment cores at Karluk (Nelson and Jordan, 1988; Knecht, 1995; Finney, 1998). Past ash falls may have affected the lake's productivity and ultimately the numbers of sockeye salmon, but no significant ash falls have occurred in the Karluk area since the inception of commercial salmon fishing. The 1912 eruption of Novarupta on the Alaska Peninsula deposited small amounts of ash in the Karluk area, even though the northern half of Kodiak Island received substantial quantities.

Since the Karluk River watershed has remained as an undeveloped wilderness for millennia, it is unlikely that local environmental changes caused the decline of its sockeye salmon.

Reduced Reproductive Capacity

Hartman and Conkle (1960) suggested that a long-term decrease in adult size and fecundity of Karluk's sockeye salmon contributed to the declining runs. While a long-term decrease in sockeye salmon length did occur during the years of commercial fishing (Fig. 4-4), egg numbers per unit of female length increased during this period (Fig. 4-8). Evidence of increased fecundity was found in 1962 and 1965 in most samples of spring-run sockeye salmon at Karluk Lake (Gard et al., 1987).

Fecundity, unadjusted for length, has not changed over the years in Karluk's sockeye salmon. Adult females of average length in the fall runs of 1903, 1926, and 1965 carried 3,500, 3,728, and 3,618 eggs respectively. That is, the reduction in female length has been offset by increased relative fecundity (Fig. 4-8). Assuming equal escapements of females to Karluk Lake, potential egg depositions at the spawning grounds were similar for both earlier and recent years. Therefore, it is unlikely that decreases in adult size and fecundity were important to the decline of sockeye salmon runs at Karluk.

Predation by Dolly Varden and Arctic Charr

Many fish species are known to prey on young sockeye salmon, but perhaps the most important in Alaska are Dolly Varden and Arctic charr. For example, Arctic charr have been reported to heavily prey on sockeye

salmon smolts in the Wood River system of Alaska (Rogers et al., 1972; Meacham and Clark, 1979). Further, Ricker (1933) reported that Dolly Varden were individually more destructive to young salmon than any other fish in Cultus Lake, British Columbia. Roos (1959), however, did not find serious charr predation on sockeye salmon in the Chignik system of Alaska.

Because of the potential losses of young salmon to fish predators, attempts were made to control Dolly Varden numbers in the Karluk River and elsewhere in Alaska during the 1920s and 1930s. Yet surprisingly, when Dolly Varden and Arctic charr food habits were studied at Karluk, DeLacy (1941) and Morton (1982) found little evidence of predation on young sockeye salmon. As a result, the theory that fish predators caused the decline of Karluk River sockeye salmon was discounted in the 1940s. But later, Rounsefell (1958) favored the fish predation theory. He cited as evidence that after 1921 the former cyclical character of Karluk's sockeye salmon runs was absent (Barnaby, 1944), in effect removing a former natural control of predator abundance. Additional evidence that fish predation might be serious was the apparent increase in freshwater mortality of young sockeye because they now resided longer in Karluk Lake. More recent USFWS studies of charr foods at Karluk Lake reinforced the general conclusions of DeLacy and Morton but also showed that predation can be intense on newly emerged sockeye fry at specific times and places, such as at Karluk Lake's outlet and the upper Karluk River during early spring (McIntyre et al., 1988). Except for those brief periods and few locations, it was difficult to find charr predation on young sockeye salmon at Karluk.

Charr and juvenile salmon have co-existed in the Karluk system for many millennia and likely have evolved adaptations to the predator-prey interaction. While charr reap huge food benefits from sockeye salmon eggs and decomposing carcasses, there is little evidence that persistent and widespread predation occurs on the juveniles. Thus, it is unlikely that charr predation caused the initial decline of Karluk River sockeye salmon.

Predation by Kodiak Brown Bear

The Karluk Lake region has long been renowned for its impressive population of brown bears, which consume large quantities of the nutrient-rich sockeye salmon from spring to autumn. Undoubtedly, the extended run season at Karluk directly benefits the region's bears. Bear predation was once thought to be a possible cause for the declining numbers of Karluk River sockeye salmon, particularly in the late 1940s. During these years, the bear population was higher than normal because of less hunting in the war years. Shuman (1950) reported that 31.3% of the dead salmon he checked at Moraine Creek had been killed unspawned by bears, and he recommended immediate control of this salmon predator. In six subsequent studies at Karluk Lake, Gard (1971) reported that 0.6–26.3% (average 9.2%) of the dead sockeye salmon had been killed unspawned by bears. The eggs lost to bear predation at Grassy Point Creek in 1964 were at most only 14% of those lost from all causes. Thus, bear predation had little adverse effect on sockeye salmon production in 1964 and was unlikely to be responsible for the long-term decline in abundance. Drucker reported heavy bear predation on sockeye salmon in Grassy Point Creek in 1968, when the salmon escapement in that stream was experimentally reduced to low levels.[5] However, he also concluded that bear predation had little effect on the total productivity of Karluk's sockeye salmon. Although bear predation on sockeye salmon might occasionally have been significant in individual spawning streams, we reject the theory that bear predation caused the long-term decline of sockeye salmon in the Karluk system.

Impediment of the Karluk River Weir on the Free Movements of Juvenile and Adult Sockeye Salmon

Van Cleve and Bevan (1973) claimed that the Karluk River weir caused the sockeye salmon run to decline after 1944. When they proposed this idea, the weir was located on the upper Karluk River, just below the lake's outlet, and was operated there each year during 1945–75. They argued that the weir interfered with the free migrations of sockeye salmon fry, smolts, and adults and thereby increased the mortality of each of these life stages. Accordingly, they recommended that all weirs be removed from the Karluk River system and that other methods be used to count adult and smolt sockeye salmon. We believe, however, that the lake outlet weir

[5] Drucker, Benson. 1973. Determining the effect of bear predation on spawning sockeye salmon on the basis of rate of disappearance of tagged salmon. (Original 1970 Title: "Extreme bear predation on sockeye salmon spawners at Grassy Point Creek, Karluk Lake, Kodiak, Alaska"). BCF, ABL, Auke Bay. Unpubl. report. 54 p. Copy in the personal papers of Richard Gard, Juneau, AK.

was an insignificant factor in the decline of the Karluk River sockeye salmon, for the reasons given below.

Some fall-run sockeye salmon spawn in the upper 5 km of the Karluk River, just downstream from the lake. Within this river section during 1945–75, spawning occurred above and below the weir. In the process of finding their natal spawning site, adults often overshoot their correct location, but then return to it a short time later. Van Cleve and Bevan claimed that some overshooting adult salmon passed through the weir and then later had difficulty bypassing the weir when they moved downstream to their spawning site. Yet direct observations of these fall-run adults in the 1960s showed that they freely moved upstream or downstream through open weir gates for much of the day. At most, the weir gates were closed between 1700 h on one day and 0800 h on the next day. When concentrations of sockeye salmon reached the weir, often two or three people counted salmon through the weir until late in the evening. During many fall days, Karluk River spawners that overshot their natal gravels moved back downstream in such abundance that total downstream weir counts were higher than upstream counts. It is unlikely that overnight delays at the weir impaired their spawning success. Likewise, adult sockeye that were destined to spawn in lake tributaries first matured for 3–5 weeks in the lake before they entered their spawning streams, and overnight delays at the weir had negligible effects on their spawning success.

Van Cleve and Bevan also believed that the weir was harmful because sockeye salmon fry that emerged from the upper Karluk River gravels had to pass upstream through the structure to reach their lake rearing habitat. They claimed that it was difficult for these young fry to negotiate the weir, possibly bruising their bodies in the process. Sockeye salmon fry that originated in the upper Karluk River were composed of two groups.[6] One group moved upstream to Karluk Lake in April and May soon after they emerged from the river gravel, while another group initially moved downstream to feed in the river and its side sloughs. The second group then moved upstream to the lake between late-July and early-September.

Most of the early upstream migrants had already moved to the lake before the weir was installed on about 20 May. Late migrants of the first fry group and the entire second group had to pass through the weir on their way to the lake. Conkle et al. (1959) found that most fry traveled upstream along the riverbanks, with the west side having 2.5 times as many fry as the east side. For most years after 1959, this upstream fry migration was assisted at the weir by 1) replacing pickets at the west bank with chicken wire and 2) placing a baffle near the east bank to reduce water velocity. Thus, the upstream fry migration proceeded without interruption or damage at the weir.

The entire out-migration of sockeye salmon smolts from Karluk Lake had to pass through the upper river weir to reach the ocean, and Van Cleve and Bevan felt that they were delayed by this structure. We observed the accumulations of smolts and Dolly Varden above the weir in the 1960s. The smolts seemed hesitant to pass through the weir and often formed large schools just upstream. As if responding to a cue, the smolt masses quickly passed downstream through the weir in one wave. Possibly, this short-term delay and concentration exposed the smolts to increased charr predation, but there is little evidence of this behavior. DeLacy (1941) and Morton (1982) found almost no charr predation on sockeye smolts during 1939–41 at the Karluk River weir, which then was located near Karluk Lagoon. Although the role of the weir in increasing predation on sockeye salmon smolts is unclear, it is noteworthy that one of the most dramatic examples of charr predation on sockeye smolts in Alaska occurred in a Bristol Bay river system lacking a weir (Rogers et al., 1972).

Competition with Sticklebacks

Threespine sticklebacks are the most abundant fish in Karluk Lake and appear to use the same habitats and foods as juvenile sockeye salmon. For many years biologists have been concerned that sticklebacks compete for food with young sockeye, thereby reducing their growth and survival. Both fish species eat planktonic crustaceans and chironomid larvae in the lake (Greenbank and Nelson, 1959; Burgner et al., 1969). In addition to similar diets, Blackett (1973) found that sticklebacks and young sockeye salmon used the same lake habitats, including the littoral zone during the fry stage and limnetic zone in the fingerling and yearling stages. He believed that sticklebacks could not be ignored as a possible factor that limited or depressed sockeye salmon productivity.

McIntyre concluded that the long-term decline of Karluk's sockeye salmon caused by commercial fishing may have let competitor species such as sticklebacks increase in abundance and further reduce sockeye

[6] See footnote 3.

salmon productivity.[7] That is, sticklebacks may have filled the ecological niche once dominated by the previously abundant juvenile sockeye. If so, the abundant stickleback population in Karluk Lake may have frustrated attempts to rehabilitate sockeye.

Wilmot and colleagues investigated the effect of stickleback competition on juvenile sockeye in the Karluk system during the 1980s.[8] They found that Karluk's sticklebacks rapidly responded to environmental changes and possibly affected the growth rates of age-0 sockeye salmon. Thus, juvenile sockeye may experience inter-specific competition during certain life stages, but the overall impact of the stickleback-sockeye interaction remains unclear. For example, although sticklebacks may have a competitive advantage in the littoral zone, it is unknown if this is true in the limnetic zone. Several current limnologists believe that juvenile sockeye salmon are superior competitors to sticklebacks. Further, recent research at Karluk Lake found little evidence of competition for the macrozooplankter *Bosmina,* a preferred food of juvenile sockeye (Sweetman and Finney, 2003).

While sticklebacks are extremely abundant in Karluk Lake, their ultimate effects on sockeye salmon abundance are unknown. Since these two fish species have interacted and adapted together in the Karluk Lake ecosystem for several thousand years, it seems highly unlikely that sticklebacks independently caused the initial decline in sockeye salmon abundance. Nevertheless, once sockeye numbers were decreased by overfishing, it remains a possibility that increasingly abundant sticklebacks in Karluk Lake hindered these salmon from quickly recovering to their former abundance.

Although competition has always been assumed to be the main stickleback-sockeye interaction, possibly another relationship is more important—stickleback abundance may depend upon the lake fertility benefits provided by salmon-carcass nutrients. This subject needs further study.

[7] McIntyre, John D. 1980. Further consideration of causes for decline of Karluk sockeye salmon. USFWS, National Fisheries Research Center, Seattle (September 18, 1980). Unpubl. report. 29 p. Located at USFWS, National Fisheries Research Center, Seattle, WA.

[8] Wilmot, R. L., R. A. Olson, R. R. Reisenbichler, J. D. McIntyre, and J. E. Finn. ca. 1989. Effects of competition with threespine stickleback *(Gasterosteus aculeatus)* on growth of age-0 sockeye salmon *(Oncorhynchus nerka)* in Karluk Lake, Alaska. USFWS, Alaska Fish and Wildlife Research Center, Anchorage, AK. Unpubl. report. 20 p. Copy from Jim Finn, USFWS, Anchorage, AK.

Karluk Lagoon Hatchery

A sockeye salmon hatchery was operated in 1891 and 1896–1916 on Karluk Lagoon, about 4 km upstream from Karluk Spit. This private hatchery was initially built to assuage anxieties that the large harvests of salmon from this one river were unsustainable. Cannery officials then firmly believed that a hatchery would support the sockeye runs and augment future commercial harvests. In spite of these goals, it has been argued that the Karluk hatchery provided almost no benefits and was partially responsible for the initial decline of these runs. Certainly, thousands of sockeye salmon were taken for hatchery brood stock and prevented from reaching their natural spawning sites at Karluk Lake. If the hatchery damaged the sockeye runs, this likely occurred for two reasons: 1) smaller escapements caused the spawning grounds at Karluk Lake to be underseeded and reduced fry production, and 2) smaller escapements decreased lake fertility by the loss of adult salmon-carcass nutrients.

A preliminary hatchery was tested on Karluk Lagoon in 1891 by an alliance of several competing canneries (known as the Karluk River Fisheries). After this one-year experiment, the APA built a larger facility in 1896, which annually incubated 24,000,000 eggs (61 troughs and 292 baskets). These initial hatchery operations were voluntary private efforts, but in 1900 the federal government mandated that canneries release four sockeye fry for each adult fish harvested. This requirement increased in 1902 to 10 fry released per adult caught, but many canneries in Alaska disregarded the law. To meet the new mandate, the APA doubled the size of its hatchery in 1903 to handle an additional 25,000,000 eggs (52 troughs and 249 baskets). As a financial incentive for canneries to operate sockeye salmon hatcheries, the federal government began in 1906 to rebate part of the taxes paid on case pack production (then 4 cents tax per case) for producing salmon fry. That is, for every 1,000 hatchery fry released, the canneries were rebated the tax on ten cases of canned salmon (40 cents).

To obtain the eggs and milt for the hatchery, 15,000 to 96,000 adult sockeye salmon were captured for brood stock each year in Karluk Lagoon (Table 11-1). Since these fish had just entered the river and were unripe, they were held to maturity in lagoon corrals or small freshwater ponds nearby the hatchery building. Eggs were stripped from mature females, fertilized, placed in hatchery baskets (80,000–103,000 eggs per basket), and incubated for several months until they

Table 11-1
Karluk Lagoon Hatchery operations, 1891–1916. Modified from Roppel (1982).

	Adults taken	Females spawned	Males spawned	Returned to river	Adult fatalities Numbers	%	Eggs taken	Fry produced Numbers	%	Commercial catch
1891							2,500,000	500,000	20	3,500,588
1896	16,697						3,260,000	2,556,440	78	2,638,976
1897	15,450	2,285					8,454,000	6,340,000	75	2,204,425
1898	55,964						4,491,000	3,369,000	75	1,534,064
1899	59,754						10,496,000	7,820,000	75	1,399,117
1900	79,752	5,524			34,141	43	19,334,000	15,566,800	81	2,594,774
1901	82,299	8,887			35,876	44	32,900,000	28,700,000	87	3,985,177
1902	77,282	5,694			28,601	37	23,400,000	17,555,000	75	2,981,112
1903							28,113,000	22,000,000	78	1,319,975
1904							45,500,000	33,670,000	74	1,638,949
1905							36,933,000	28,236,412	76	1,787,642
1906	80,347	13,037	11,120	19,594	36,596	46	38,696,200	33,844,000	87	3,382,913
1907	95,734	15,507	14,720	14,258	51,249	54	47,808,200	37,250,000	78	2,929,886
1908	71,320	14,074	12,588	9,135	35,523	50	40,320,000	30,700,000	76	1,608,418
1909	95,804	15,144	14,075	6,628	59,957	63	45,228,000	30,500,000	67	923,501
1910	85,623	17,881	17,390	8,178	42,174	49	49,626,000	31,150,000	63	1,492,544
1911	79,699	14,516	14,770	4,747	30,786	39	41,026,800	34,495,000	84	1,723,132
1912	69,053	14,219	14,929	8,794	31,111	45	45,500,000	41,803,155	92	1,245,275
1913	62,507	11,138	11,997	5,149	34,223	55	34,629,160	31,546,000	91	868,422
1914	59,684	11,900	11,624	1,073	35,087	59	30,240,000	27,704,000	92	540,455
1915	87,091	15,698	16,098	4,673	50,622	58	41,135,000	23,948,000	58	828,429
1916							1,016,000			2,343,104
Total	1,174,060	165,504	139,311	82,229	505,946	43	630,606,360	489,253,807	78	43,470,878

hatched. Fry were then released into Karluk Lagoon. During the 22 years of hatchery operations, about 630,000,000 sockeye eggs were taken and 489,000,000 fry were released.

Competition for salmon was intense in the early fishery, and nonstop beach seining at Karluk Spit often barred fish from entering the river. Sockeye that escaped the fishery next passed through the upper lagoon, where some were taken for hatchery brood stock. At times the intense harvests near Karluk Spit made it difficult for the hatchery to procure enough adults. In 1896 a barricade was temporarily placed across the Karluk River to help the hatchery catch brood fish, but rival canneries soon removed it (Tingle, 1897). Commercial fishing was outlawed in the lagoon in 1898, but was allowed there for the hatchery and Karluk's native residents.

Two major problems plagued the Karluk Lagoon hatchery: adult mortality during the maturation period and fry survival in the estuarine rearing waters. Both problems arose because of ignorance about the life history of sockeye salmon. Although hatchery records are incomplete, at least 1,200,000 adult sockeye were taken by the hatchery during its 22 years of operation. Nearly half of these fish died in the maturation corrals and ponds before they spawned (Table 11-1). Additional uncounted fish were lost from those detained several weeks in hatchery enclosures and then later released after the hatchery had reached full egg capacity. Governmental officials and inspectors initially praised the APA hatchery, but soon were upset by the high mortality of brood fish.

The many millions of hatchery fry released into Karluk Lagoon probably had little effect on Karluk's sockeye salmon run, though the ultimate fate of these young fish is unknown. During the early hatchery years, everyone thought that released fry quickly moved through the lagoon to their supposed rearing habitat in the ocean. But after Chamberlain (1907) discovered that juvenile sockeye reared in freshwaters for at least a year before they migrated to the ocean, doubts began to arise about the survival of fry released into the lagoon. Since the environmental conditions there now seemed to be entirely unsuitable for fry to grow and prosper, it quickly became the consensus that the APA hatchery was poorly located—it should have been built at the lake. As a result, the hatchery came under increasing criticism during its later years, especially after Charles Gilbert confirmed by scale analysis that juvenile sockeye reared for several years in Karluk Lake before they

entered the ocean.[9] The APA hatchery on Karluk Lagoon permanently ceased operations on 30 June 1916.[10]

Potentially, the APA hatchery may have aggravated the long-term decline of sockeye salmon by reducing the escapements below that needed to completely seed the spawning grounds at Karluk Lake. Over its years of operation, the hatchery annually prevented, on average, about 50,000 adult sockeye from spawning at the lake. The true significance of this loss of natural spawning and fry production is unknown because escapement data were not measured during 1891–1916. Even qualitative estimates were rare during this period since biologists and officials seldom visited the lake spawning grounds. Continued large commercial harvests during these years suggest that the sockeye runs remained strong and escapements probably were adequate (Table 11-1). Fishery inefficiencies and closures for one day per week allowed at least some adult sockeye salmon to reach the lake during this early era. Rutter's counts of the sockeye spawning in Moraine Creek in 1903 suggested that this stream was well seeded, even though the overall run that year was smaller than normal.[11] USBF biologist Bower reported that an enormous number of sockeye salmon spawned at Karluk Lake in July–August 1911 (Bower, 1912; U.S. Senate, 1912).

Besides these direct observations that natural spawning at the lake was adequate during the hatchery era, a unique spawning feature of the Karluk system also suggests that escapements then may have been sufficient. The total spawning area at Karluk Lake is limited and could have been fully seeded by much smaller runs than were indicated by the 1891–1916 harvests. Studies done at Karluk in the 1960s–1970s found that the total spawning area for this system was fully seeded by about 350,000–800,000 fish. When 2,500,000 sockeye reached the lake in 1926, the spawning grounds were over-seeded and many eggs were wasted.[12] While it still remains possible that escapements were too low for complete seeding during 1891–1916, the annual loss of 50,000 hatchery fish was only 3% of those lost to the commercial fishery (about 2,000,000 per year). From this limited evidence, we discount the notion that the hatchery significantly reduced natural fry production because the spawning areas were under-seeded.

Another possibility is that the APA hatchery reduced the lake's fertility by keeping adult sockeye from reaching the lake and adding their carcass nutrients. Between 1891 and 1916 the hatchery took about 1,200,000 adult sockeye, but during the same period the commercial fishery harvested over 43,000,000 fish (Table 11-1). When these two nutrient losses are compared, the reduction in lake fertility caused by the hatchery was a small fraction of that lost in the commercial fishery and does not appear to be of lasting significance.

One long-term consequence of the APA hatchery at Karluk is that the 22 years of fry releases established a unique small subpopulation of lagoon-spawning sockeye salmon. Reportedly, a few hundred or thousand lagoon-spawning sockeye have been annually observed throughout most of Karluk's research history. The first such record of this spawning came in 1901, just a few years after the 1896–1897 fry releases (Kutchin, 1902). Hatchery superintendent Richardson once observed sockeye salmon spawning under the ice in Karluk Lagoon in February.[13]

Ocean Climate—Lake Fertility

While most theories of population regulation have focused on various freshwater factors, the ocean climate–lake fertility theory is based on the premise that sockeye salmon abundance is determined by the success of two very different life stages, the smolt-to-adult phase in the marine environment and the egg-to-smolt phase in the freshwater habitat. Although fragments of this theory can be traced back many years, its modern essentials come from several lines of research during in the 1980s–1990s. One source was the growing evidence that many Pacific salmon populations are greatly influenced by large-scale ocean climates (Beamish and Bouillon, 1993; Martinson et al., 2008, 2009a, b), though the exact regulatory mecha-

[9] Memo (16 April 1916) from Ward T. Bower, USBF, Washington, DC, to Commissioner of Fisheries, Washington, DC. Located at Alaska Historical Collections, Alaska State Library, Juneau, AK.

[10] Memo (23 July 1916) report from E. M. Ball, Assistant Agent, Alaska Fisheries Service, USBF, Washington, DC, to Commissioner of Fisheries, Washington, DC. Located at Alaska Historical Collections, Alaska State Library, Juneau, AK.

[11] Rutter, Cloudsley Louis. 1903. Field notes by Cloudsley Rutter on his Karluk work of 1903. Unpubl. notes. 48 p. Copy provided by Mark R. Jennings (Davis, CA) and located in Box 130, Barton Warren Evermann papers, Library Special Collections, California Academy of Sciences, San Francisco, CA.

[12] See footnote 1.

[13] See footnote 11.

nisms are unclear. In freshwater, several studies of the limnology, marine-derived nutrients, and paleolimnology of Karluk Lake have demonstrated the importance of escapement size and salmon-carcass nutrients to lake fertility and the forage base that supports juvenile sockeye salmon (Koenings and Burkett, 1987b; Schmidt et al,. 1998; Finney, 1998; Finney et al. 2000, 2002; Kline 1993, 2003).

The ocean climate–lake fertility theory can best be described by discussing the dynamics of sockeye salmon runs during: 1) the natural pre-fishery conditions that existed for many millennia and 2) the commercial fishing years that began in 1882.

1) Natural Pre-Fishery Conditions

For most of its recent evolutionary history of some 10,000 years, the abundance of Karluk's sockeye salmon has varied according to natural environmental factors in both the marine and freshwater phases of its life cycle. Although the Alutiiq people of Kodiak Island had annually captured sockeye salmon at Karluk for many millennia, their total harvests are assumed to be relatively small in comparison to the total run size and are not a significant factor that affected sockeye abundance.

When sockeye salmon smolts enter the ocean, their ability to survive to adulthood is partially governed by their size and condition, both qualities determined in freshwater. Since Karluk Lake typically produces relatively large smolts, they tend to have rather high survival rates in the ocean. When this fact was first discovered in the 1920s, it was then assumed that the ocean environment, where sockeye salmon feed and grow for a year or more before reaching maturity, was relatively benign. Nevertheless, the ocean is not a constant environment that always returns the same proportion of smolts as adults each year. In fact, adult returns are governed by ocean phenomena that are currently not well understood, though large-scale climatic factors that affect the forage base are important. When ocean climates vary between benign and adverse conditions, smolt-to-adult survival rates are affected. Paleolimnological records from Karluk Lake sediment cores indicate that variations in ocean climate can last a few years, or for many centuries, and that these shifts can significantly impact sockeye salmon abundance. Thus, the number of adult sockeye salmon that return to the Karluk River each year is determined by the abundance and condition of the smolts produced by the lake and by ocean climatic factors.

When adult sockeye salmon leave the ocean to spawn in their natal freshwaters, they transport upstream not only their eggs and milt, but significant quantities of marine-derived nutrients in their body tissues. These nutrients, such as nitrogen and phosphorus, are released into the freshwater environment when salmon carcasses decompose. Released nutrients are soon incorporated into the surrounding biota, first by microorganisms such as the lake's phytoplankton and then via the food chain into zooplankton and juvenile sockeye. Thus, besides the genetic connection between adult and juvenile sockeye, there also exists a nutrient link between adult and juvenile success. The addition of salmon-carcass nutrients influences the ability of Karluk Lake to produce numerous high-quality smolts. That is, adult sockeye salmon not only use freshwater for their spawning, but by adding their nutrients they significantly modify the capacity of the lake rearing habitat to produce the zooplankton consumed by their offspring. The fertility of Karluk Lake is sensitive to salmon-carcasses because this biotic nutrient source often supplies a major proportion of the total annual loading of important elements, while lesser amounts come from watershed and rainfall sources.

The natural nutrient transfer between adult and juvenile sockeye salmon, and between the ocean and freshwater environments, apparently operates by a positive feedback mechanism. That is, when ocean conditions are favorable, adult returns and nutrient inflows increase to Karluk Lake, enhancing the lake's fertility, forage base, juvenile growth, smolt production, and future adult returns. With such a reinforcing cycle, the success of young sockeye is dependent on the nutrients provided by adults, while adult returns are partially dependent on juvenile success. Conversely, when ocean conditions are adverse, adult returns and nutrient inflows decrease to the lake, reducing its fertility, forage base, juvenile growth, smolt production, and future adult returns.

No matter how advantageous the lake may be in producing sockeye smolts, it can be overridden by adverse ocean climates that result in fewer returning adults. If favorable or adverse conditions last for decades or centuries, positive feedback can greatly increase or decrease the sockeye salmon runs as they adjust to a new level of lake fertility. Change in sockeye salmon abundance is moderated during short-term fluctuations in ocean climate by internal system inertia. Above a certain baseline that is determined by watershed and rainfall nutrient inflows to the lake, ocean

climatic factors act as the ultimate control of both lake fertility and sockeye salmon abundance at Karluk.

2) Commercial Fishing Since 1882

Once commercial fishing for sockeye salmon began at Karluk in 1882, especially for the first 20–30 years of huge harvests, the nutrient link and positive feedback mechanism were disrupted. Salmon-carcass nutrients that would have bolstered the fertility of Karluk Lake and its future runs were removed by the commercial fishery. The ability of adult sockeye to transfer significant nutrient benefits to their offspring was greatly diminished. Consequently, the lake's productivity began to decline, though because of the inherent inertia within this system, it was a number of decades before the adverse effects became evident on the sockeye salmon runs (Fig. 1-2). The oligotrophication of Karluk Lake resulted in nearly 100 years of declining and diminished sockeye salmon runs, which were aggravated in the 1960s–1970s by adverse ocean climates. The downward trend in Karluk's sockeye salmon runs was reversed in the 1980s–1990s by a combination of management for higher escapements, artificial fertilization of the lake, and a favorable shift in the marine climate (Fig. 1-3).

Conclusions

Many theories have been proposed over the years to explain the long-term decline and subsequent recovery of sockeye salmon abundance at Karluk. While many theories retain at least some possibility of truth, we believe that the ocean climate–lake fertility theory best explains the long-term variations in sockeye salmon abundance at Karluk. The nearly 100-year decline in sockeye numbers was primarily precipitated by overfishing in the commercial fishery. This effect continued for many years and was aggravated by several decades of adverse ocean climates. We believe the mechanism by which overfishing caused the decline was not from insufficient spawning, but from changes to the fertility of Karluk Lake and disruption of the positive feedback mechanism. Commercial harvests greatly reduced the quantities of nutrients released back to the lake each year in the decomposing bodies of sockeye salmon adults. The productivity of Karluk Lake appears to be sensitive to these annual inputs of biotic nutrients. The recovery of sockeye salmon abundance since 1985 was accomplished by increasing the lake's fertility with higher escapements, artificial fertilizations, and a favorable shift in the ocean climate. In contrast, most of the other proposed theories do not explain the recovery since 1985. It appears that maintenance of Karluk Lake's long-term productivity requires higher sockeye escapements than are needed to fully seed the spawning grounds.

Once sockeye salmon numbers were greatly reduced by overfishing at Karluk, it is likely that normal biological processes and interactions that had been determined over a long evolutionary history were altered. Several of the theories are implausible as initiators of the long-term decline of Karluk's sockeye salmon, though they possibly had some influence as the decrease continued. These include the theories on local changes in the physical environment, reduced reproductive capacity, charr predation, bear predation, weir impediments, stickleback competition, and hatchery operations.

Literature Cited

Alaska Department of Fish and Game.

ca. 1988. Proceedings of the 1988 Alaska Sockeye Culture Workshop, Ketchikan, Alaska, July 12–13, 1988. Alaska Dep. Fish Game, Div. Fish. Rehab., Enhance., and Dev., Juneau.

1995. Kodiak Management Area annual salmon management report 1986 and 1987. Alaska Dep. Fish Game, Div. Commercial Fish., Kodiak. Regional Info. Rep. 4K95-5.

1998. 1996–1998 Cook Inlet, Kodiak, and Chignik Areas Commercial Fishing Regulations. Alaska Dep. Fish Game, 90 p.

Alaska Territorial Legislature.

1949. House Memorial Number 3. Territory of Alaska, Session Laws, Resolutions, and Memorials passed by the 19th regular session of the Territorial Legislature, 622 p. Territory of Alaska, Juneau.

1951. House Memorial Number 6. Territory of Alaska, Session Laws, Resolutions, and Memorials passed by the 20th regular session of the Territorial Legislature, 693 p. Territory of Alaska, Juneau.

Allen, Durward L.

1954. Our wildlife legacy, 422 p. Funk and Wagnalls Company, New York.

Anas, R. E., and J. R. Gauley.

1956. Blueback salmon, *Oncorhynchus nerka,* age and length at seaward migration past Bonneville Dam. U.S. Dep. Fish Wildl. Serv., SSRF 185, 46 p.

Andrievskaya, L. D.

1957. [The food of the Pacific salmon in the northwestern Pacific Ocean] Materialy po Biologii Morskovo Perioda Zhizni Dalnevostochnykh Lososei. VNIRO, Moscow: 64–75. (Fish. Res. Board Can., Transl. Ser. No. 182)

Atwell, Gerry.

1975. Karluk Lake breakup. Alaska 41(5):47.

Bams, R. A.

1969. Adaptations of sockeye salmon associated with incubation in stream gravels. *In* Symposium on Salmon and Trout in Streams, T. C. Northcote (ed.), p. 71–87. H. R. MacMillan Lectures in Fisheries. Inst. Fish., Univ. British Columbia, Vancouver.

Barnaby, Joseph Thomas.

1932. The growth of the red-salmon (*Oncorhynchus nerka,* Walbaum) of the Karluk River and the growth of its scales. MA thesis, 50 p. Dep. Zoology, Leland Stanford Junior Univ., CA.

1944. Fluctuations in abundance of red salmon, *Oncorhynchus nerka,* (Walbaum), of the Karluk Lake, Alaska. Fish. Bull. 50(39):237–295.

Barnes, Victor G., Jr.

1990. The influence of salmon availability on movements and range of brown bears on southwest Kodiak Island. Int. Conf. Bear Res. Manage. 8:305–313.

Barr, Claude H.

1931. Karluk Kodiaks. Outdoor Life 67(3):11–13, 84–87.

Barrett, Bruce M.

1989. North Shelikof Strait 1988 sockeye catch—distribution, timing, and stock composition. Alaska Dep. Fish Game, Div. Commercial Fish., Reg. Info. Rep. 4K88-6 (March 1989), 38 p.

Barrett, Bruce M., and Patricia A. Nelson.

1994. Estimated run timing of selected sockeye salmon stocks on the west and east sides of Kodiak Island. Alaska Dep. Fish Game, Commercial Fish. Manage. Dev. Div., Reg. Info. Rep. 4K94-6, 53 p.

1995. Estimation of Karluk Lake early and late run sockeye returns based on scale age data, 1985–1994. Alaska Dep. Fish Game, Commercial Fish. Manage. Dev. Div., Reg. Info. Rep. 4K95-44 (Nov. 1995), 46 p.

Beamish, Richard J., and Daniel R. Bouillon.

1993. Pacific salmon production trends in relation to climate. Can. J. Fish. Aquat. Sci.50:1002–1016.

Bean, Tarleton H.

1882. Notes on birds collected during the summer of 1880 in Alaska and Siberia. Proc. U.S. Natl. Mus. 5:144–175.

1887. The fishery resources and fishing-grounds of Alaska. *In* The fisheries and fishery industries of the United States, Section III, The fishing grounds of North America, by G. B. Goode, p. 81–115. U.S. Comm. Fish Fisheries, Govt. Print. Off., Washington, DC.

1889. Bears, birds and fishes. Forest and Stream 33 (18 and 19):348, 368.

1890. The Alaskan salmon and their allies. Trans. Am. Fish. Soc. 1890:49–66.

1891. Report on the salmon and salmon rivers of Alaska, with notes on the conditions, methods, and needs of the salmon fisheries. Bull. U.S. Fish Comm., Vol. 9, for 1889:165–208.

1894. Life history of the salmon. *In* Report on the salmon fisheries of Alaska, by Marshall McDonald, p. 21–38. Bull. U.S. Fish Comm., Vol. 12, for 1892, 49 p. The Miscellaneous Documents (No. 122) of the House of Representatives for the Second Session of the Fifty-Third Congress, 1893–1894. Vol. 18.

1902. A naturalist's adventures. *In* The white world: Life and adventures within the Arctic Circle portrayed by famous living explorers, by Rudolf Kersting, p. 241–266. Issued under the auspices of the Arctic Club. Lewis, Scribner, and Co., New York, 386 p.

Begich, Robert N.

1995. Assessment of the 1994 return of steelhead to the Karluk River, Alaska. Alaska Dep. Fish Game, Div. Sport Fish, Fishery Data Series No. 95-41 (Dec. 1995), 63 p.

Berns, Vernon D., Gerry C. Atwell, and Daniel L. Boone.

1980. Brown bear movements and habitat use at Karluk Lake, Kodiak Island. Bear Biol. Assoc. Conf. Ser. 3, Int. Conf. Bear Res. Manage. 4:293–296.

Bevan, Donald E.

1953. Karluk Lake stream surveys, 1952. Univ. Wash.,

Fish. Res. Inst., Circ. No. 43, Kodiak Island Memo. No. 8 (February 23, 1953), 27 p.
1959. Tagging experiments in Kodiak Island area with reference to the estimations of salmon (*Oncorhynchus*) populations. Ph.D. thesis, 173 p. Univ. Wash., Seattle.
1962. Estimation by tagging of the size of migrating salmon populations in coastal waters. *In* Studies of Alaska red salmon, T. S. Y. Koo (ed.), p. 377–449. Univ. Wash. Publ. in Fish., New Ser. 1, 449 p.

Bevan, Donald E., and Charles E. Walker.
1954. Karluk Lake stream surveys, 1953. Univ. Wash., Fish. Res. Inst., Circ. No. 59, Kodiak Memo. No. 11 (February 1, 1954), 41 p.
1955. Karluk Lake observations, 1954. Univ. Wash., Fish. Res. Inst., Circ. No. 78, Kodiak Memo. No. 14 (January, 1955), 47 p.

Bilton, H. T.
1971. A hypothesis of alternation of age of return in successive generations of Skeena River sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 28:513–516.

Bilton, H. T., and S. A. M. Ludwig.
1966. Times of annulus formation on scales of sockeye, pink, and chum salmon in the Gulf of Alaska. J. Fish. Res. Board Can. 23:1403–1410.

Bilton, H. T., M. Flain, F. Lucas, P. Kearton, and Richard Gard.
1983. Tests on the accuracy of ageing New Zealand quinnat salmon (*Oncorhynchus tshawytscha*) from their scales. Can. Fish. Aquat. Sci., Tech. Rep. No. 1199, 16 p.

Birge, E. A., and W. H. Rich.
1927. Observations on Karluk Lake, Alaska. Ecology 8(3):384.

Black, Charles Spurgeon.
1929. Chemical analyses of lake deposits. Trans., Wisconsin Acad. Sci., Arts and Letters 24:127–133.

Blackett, Roger F.
1968. Kodiak Island sockeye salmon investigations. Alaska Dep. Fish Game, Annual Progr. Rep., Anadromous Fish Project (AFC-8-1), 9 p.
1973. Kodiak sockeye rehabilitation, 1971 and 1972 field seasons. Alaska Dep. Fish Game, Juneau, Completion Rep., Anadromous Fish Project AFC-27 (May 1973), 148 p.

Blackett, Roger F., and Alan Davis.
1971. Kodiak sockeye rehabilitation, 1970 field season. Alaska Dep. Fish Game, Juneau, Annual Tech. Rep., Anadromous Fish Project (AFC-27), 123 p.

Blackett, Roger F., and M. F. Eaton.
1968. Kodiak Island sockeye salmon investigations. Alaska Dep. Fish Game, Annual Tech. Rep., Anadromous Fish Project (AFC-8-1), 61 p.

Blackett, Roger F., Robert C. Lebida, and Louis A. Gwartney.
1969. Kodiak Island sockeye salmon investigations, 1968 field season. Alaska Dep. Fish Game, Annual Tech. Rep., Anadromous Fish Project (AFC-8-2), 104 p.

Blackett, Roger F., R. Alan Davis, and P. A. Russell.
1970. Kodiak Island sockeye salmon investigations, 1969 field season. Alaska Dep. Fish Game, Annual Tech. Rep., Anadromous Fish Project (AFC-8-3), 194 p.

Bower, Ward T.
1912. Fish culture in Alaska. *In* Alaska fisheries and fur industries in 1911, by Barton Warren Evermann, p. 66–88. U.S. Dep. Commerce and Labor, Bur. Fish., Doc. No. 766, 99 p.
1922. Alaska fishery and fur-seal industries in 1921. U.S. Dep. Commerce, Bur. Fish., Appendix X to Report of Commissioner of Fisheries for 1922, Bur. Fish. Doc. No. 933.
1937. Alaska fishery and fur-seal industries in 1936. U.S. Dep. Commerce, Bur. Fish., Admin. Rep. No. 28, Appendix II to Report of Commissioner of Fisheries for the fiscal year 1937.
1941. Alaska fishery and fur-seal industries in 1939. U.S. Dep. Interior, Bur. Fish., Admin. Rep. No. 40, Appendix II to Report of Commissioner of Fisheries for the fiscal year 1939.
1944. Alaska fishery and fur seal industries: 1942. U.S. Dep. Interior, Fish Wildl. Serv., Stat. Dig. No. 8, 52 p.

Bradley, J. Chester.
1908. Notes on two amphipods of the genus *Corophium* from the Pacific Coast. Univ. Calif. Publ. in Zoology 4(4):227–252.

Brannon, E. L.
1972. Mechanisms controlling migration of sockeye salmon fry. Int. Salmon Fish. Comm. Bull. 21, 86 p.
1987. Mechanisms stabilizing salmon fry emergence timing. *In* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management, H. D. Smith, L. Margolis, and C. C. Wood (eds.), p. 120–124. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Brennan, Kevin.
1995. Kodiak Management Area commercial salmon annual management report, 1993. Alaska Dep. Fish Game, Commercial Fish. Manage. Dev. Div., Reg. Info. Rep. No. 4K95-3.
1998. Kodiak Management Area commercial salmon annual management report, 1996. Alaska Dep. Fish Game, Commercial Fish. Manage. Dev. Div., Reg. Info. Rep. No. 4K98-35 (June 1998).
2000. Kodiak Management Area commercial salmon annual management report, 1997. Alaska Dep. Fish Game, Div. Commercial Fish., Reg. Info. Rep. No. 4K00-27.
2001. Kodiak Management Area commercial salmon annual management report, 2001. Alaska Dep. Fish Game, Div. Commercial Fish., Reg. Info. Rep. No. 4K01-62.

Brennan, Kevin, Larry Malloy, Dave Prokopowich, and Dennis Gretsch.
1992. Kodiak Management Area annual salmon management report, 1989. Alaska Dep. Fish Game, Div. Commercial Fish., Reg. Info. Rep. No. 4K92-30 (Aug. 1992), 262 p.

Brennan, Kevin, David Prokopowich, and Dennis Gretsch.
1993. Kodiak Management Area, commercial salmon annual management report, 1992. Alaska Dep. Fish

Game, Div. Commercial Fish., Reg. Info. Rep. No. 4K93-28 (Oct. 1993), 278 p.
Brennan, Kevin, Dave Prokopowich, and Dennis Gretsch.
1996. Kodiak Management Area commercial salmon annual management report, 1994. Alaska Dep. Fish Game, Commercial Fish. Manage. Dev. Div., Reg. Info. Rep. No. 4K96-38 (July 1996), 277 p.
1997. Kodiak Management Area commercial salmon annual management report, 1995. Alaska Dep. Fish Game, Commercial Fish. Manage. Dev. Div., Reg. Info. Rep. No. 4K97-30.
Brittan, Martin R.
1997. The Stanford School of Ichthyology: Eighty years (1891–1970) from Jordan (1851–1931) to Myers (1905–1985) *In* Collection building in ichthyology and herpetology, Theodore W. Pietsch and William D. Anderson, Jr. (eds.), p. 233–264. Am. Soc. Ichthyol. Herpetol., Spec. Publ. No. 3, 593 p. Allen Press Inc., Lawrence, KS.
Brodie, Joan R.
1996. Kodiak Management Area salmon escapement cumulative counts for fish-weirs, 1987–1996. Alaska Dep. Fish Game, Commercial Fish. Manage. Dev. Div., Reg. Info. Rep. No. 4K96-51 (Nov. 1996), 175 p.
Brodie, Joan R., Kevin R. Brennan, and Larry Malloy.
1997. Kodiak Management Area annual commercial and subsistence salmon management report, 1990. Alaska Dep. Fish Game, Commercial Fish. Manage. Dev. Div., Reg. Info. Rep. No. 4K97-5.
Bruce, Miner W.
1895. Alaska: Its history and resources, gold fields, routes and scenery, 128 p. Lowman, and Hanford Stationery and Printing Co., Seattle, WA.
Burgner, Robert L.
1962. Studies of red salmon smolts from the Wood River Lakes, Alaska. *In* Studies of Alaska red salmon, T. S. Y. Koo (ed.), p. 247–314. Univ.Wash. Publ. Fish., New Ser. 1, 449 p.
1991. Life history of sockeye salmon (*Oncorhynchus nerka*). *In* Pacific salmon life histories, C. Groot and L. Margolis (eds.), p. 1–117. Univ. British Columbia Press, Vancouver, BC, 564 p.
Burgner, Robert L., Charles J. Di Costanzo, Robert J. Ellis, George Y. Harry, Jr., Wilbur L. Hartman, Orra E. Kerns, Jr., Ole A. Mathisen, and William F. Royce.
1969. Biological studies and estimates of optimum escapements of sockeye salmon in the major river systems in Southwestern Alaska. Fish. Bull. 67(2):405–459.
Caldentey, Iris O.
2007. Kodiak commercial fisheries salmon management field camp and weir operational plan, 2008. Alaska Dep. Fish Game, Div. Commercial Fish., Reg. Info. Rep. No. 4K08-01 (December 2007), 43 p.
2009a. Kodiak Management Area salmon daily and cumulative escapement counts for river systems with fish weirs, 1999–2008. Alaska Dep. Fish Game, Div. Sport Fish and Commercial Fish., Fish. Manage. Rep. No. 09-18 (April 2009), 198 p.
2009b. Kodiak commercial fisheries salmon management field camp and weir operational plan, 2009. Alaska Dep. Fish Game, Div. Sport Fish and Commercial Fish., Reg. Info. Rep. No. 4K09-08 (June 2009), 56 p.
Chamberlain, F. M.
1907. Some observations on salmon and trout in Alaska. U.S. Dep. Commerce and Labor, Bur. Fish. Rep. Comm. Fish. for the fiscal year 1906 and special papers. Bur. Fish. Doc. No. 627 (December 18, 1907), 112 p.
Clark, Donald W.
1984. Pacific Eskimo: historical ethnography. *In* Arctic, David Damas (ed.), p. 185–197. Handbook of North American Indians, Vol. 5, William C. Sturtevant (general ed.), 829 p. Smithsonian Institution, Washington, D.C.
Clark, John H., Andrew McGregor, Robert D. Mecum, Paul Krasnowski, and Amy M. Carroll.
2006. The commercial salmon fishery in Alaska. Alaska. Fish. Res. Bull. 12(1):1–146.
Clark, Webster K.
1959. Kodiak bear—red salmon relationships at Karluk Lake, Alaska. Trans. North Am. Wildl. Conf. 24:337–345.
1965. Bear study—Karluk Lake, 1955. U.S. Dep. Interior, Fish Wildl. Serv., Bur. Commercial Fish., Auke Bay Biol. Lab., Manuscr. Rep.–File, MR-F 10, 41 p.
Conkle, Charles Y., Robert F. Raleigh, and John B. Owen.
1959. Salmon survival investigations. Sockeye salmon survival studies at Karluk Lake, Kodiak Island, 1958. U.S. Dep. Interior, Fish Wildl. Serv., Bur. Commercial Fish., Alaska Region, Manuscr. Rep.–File, MR-F 23 (June 11, 1959), 82 p.
Connelly, Dolly.
1969. Mighty hunter. The Blade, Sunday Magazine, Toledo, Ohio (8 June 1969):30–31, 34–39.
Croasdale, Hannah T.
1958. Freshwater algae of Alaska. 2. Some new forms from the plankton of Karluk Lake. Trans. Am. Microscopical Soc. 77(1):31–35.
Crowell, Aron L., Amy F. Steffian, and Gordon L. Pullar (editors).
2001. Looking both ways: heritage and identity of the Alutiiq people, 265 p. Univ. Alaska Press, Fairbanks.
Davydov, G. I.
1977. Two voyages to Russian America, 1802–1808, Colin Bearne (translator) and Richard A. Pierce (ed.). Materials for the Study of Alaska History No. 10, 257 p. The Limestone Press, Kingston, Ontario.
DeLacy, Allan Clark.
1941. Contributions to the life histories of two Alaskan charrs, *Salvelinus malma* (Walbaum) and *Salvelinus alpinus* (Linnaeus). Ph.D. thesis, 114 p. Univ. Wash., Seattle.
DeLacy, Allan C., and W. Markham Morton.
1943. Taxonomy and habits of the charrs, *Salvelinus malma* and *Salvelinus alpinus, of* the Karluk drainage system. Trans. Am. Fish. Soc. 72: 79–91.
Dell, M. B.
1963. Oceanic feeding habits of the sockeye salmon, *Oncorhynchus nerka* (Walbaum), in Aleutian waters. MA thesis, 40 p. Univ. Michigan, Ann Arbor.

Denning, D. G.
1951. Records and descriptions of Nearctic caddisflies. J. Kansas Entomol. Soc. 24(4):157–162.
Dinnocenzo, Joe.
2006. Kodiak Management Area commercial salmon annual management report, 2004. Alaska Dep. Fish Game, Fish. Manage. Rep. No. 06-14 (March 2006), 194 p.
2010. Kodiak Management Area commercial salmon fishery annual management report, 2008. Alaska Dep. Fish Game, Fishery Management Report No. 10-02 (February 2010), 182 p.
Dinnocenzo, Joe, and Iris O. Caldentey.
2008. Kodiak Management Area commercial salmon fishery annual management report, 2007. Alaska Dep. Fish Game, Fishery Management Report No. 08-45 (September 2008), 178 p.
Dinnocenzo, Joe, Geoff Spalinger, and Jeff Wadle.
2006. Kodiak Management Area commercial salmon fishery annual management report, 2005. Alaska Dep. Fish Game, Fishery Management Report No. 06-53 (Oct. 2006), 197 p.
2007. Kodiak Management Area commercial salmon fishery annual management report, 2006. Alaska Dep. Fish Game, Fishery Management Report No. 07-25 (Apr. 2007), 188 p.
Dinnocenzo, Joe, Geoff Spalinger, and Iris O. Caldentey.
2010. Kodiak Management Area commercial salmon fishery annual management report, 2009. Alaska Dep. Fish Game, Fishery Management Report No. 10-22 (May 2010), 188 p.
Dmytryshyn, Basil, and E. A. P. Crownhard-Vaughan.
1979. The end of Russian America, Captain P.N. Golovin's last report, 1862, 249 p. Oregon Historical Society, Portland.
Dodge, Harry B., III.
2004. Kodiak Island and its bears: A history of bear/human interaction on Alaska's Kodiak Archipelago, 352 p. Great Northwest Publishing and Distributing Company Inc., Anchorage, AK.
Drucker, Benson.
1968. Red salmon studies at Karluk Lake, 1967. U.S. Dep. Interior, Fish Wildl. Serv., Bur. Commercial Fish., Auke Bay Biol. Lab., Manuscr. Rep. 1968, MR 68-7 (May 1, 1968), 36 p.
1970. Red salmon studies at Karluk Lake, 1968. U.S. Dep. Interior, Fish Wildl. Serv., Bur. Commercial Fish., Auke Bay Biol. Lab., Manuscr. Rep. 1970, MR 70-1 (March 10, 1970), 55 p.
1971. Bibliography of biological and related studies carried out at Karluk and Bare Lakes, Kodiak Island, Alaska—1891 to 1970. Natl. Mar. Fish. Serv., Auke Bay Biol. Lab., Manuscr. Rep.–File, MR-F No. 89 (May 10, 1971), 16 p.
1972. Some life history characteristics of coho salmon of the Karluk River System, Kodiak Island, Alaska. Fish. Bull. 70(1):79–94.
Drucker, Benson, and Richard Gard.
1967. Red salmon studies at Karluk Lake, 1966. U.S. Dep. Interior, Fish Wildl. Serv., Bur. Commercial Fish., Auke Bay Biol. Lab., Manuscr. Rep. 1967, MR 67-5 (March 15, 1967), 31 p.
Dufresne, Frank.
1951. Is Alaska's Kodiak doomed? Field and Stream (June 1951) 56(2):30–31, 112–113.
Dunn, J. Richard.
1996. Charles Henry Gilbert (1859–1928): An early fishery biologist and his contributions to knowledge of Pacific salmon (*Oncorhynchus* spp.). Reviews in Fishery Sci. 4(2):133–184.
1997. Charles Henry Gilbert (1859–1928): Pioneer ichthyologist of the American west. *In* Collection building in ichthyology and herpetology, Theodore W. Pietsch and William D. Anderson, Jr. (eds.), p. 265–278. Am. Soc. Ichthyol. Herpetol., Spec. Publ. No. 3, 593 p. Allen Press Inc., Lawrence, KS.
2001a. William Francis Thompson (1888–1965): a preeminent fishery biologist of the early and mid twentieth century. Mar. Fish. Rev. 63(2):1–4.
2001b. William Francis Thompson (1888–1965) and his pioneering studies of the Pacific halibut, *Hippoglossus stenolepis*. Mar. Fish. Rev. 63(2):5–14.
2001c. William Francis Thompson (1888–1965) and the dawn of marine fisheries research in California. Mar. Fish. Rev. 63(2):15–24.
Earle, F. S.
1904. Proceedings of the Club, Tuesday, December 8, 1903. Torreya 4(1):12–15.
Earp, B. J., and R. L. Schwab.
1954. An infestation of leeches on salmon fry and eggs. Prog. Fish-Cult. 16:122–124.
Eicher, George .J., Jr., and George A. Rounsefell.
1957. Effects of lake fertilization by volcanic activity on abundance of salmon. Limnol. Oceanogr. 2:70–76.
Eifert, Virginia S. (ed.).
1941. The bears of Kodiak. The Living Museum 3(6):42.
Ellis, Robert J.
1963. The abundance and distribution of juvenile red salmon and associated species in lakes of the Naknek River system and Karluk Lake. U.S. Dep. Interior, Fish Wildl. Serv., Bur. Commercial Fish., Auke Bay Biol. Lab., Manuscr. Rep. 1963, MR 63-2 (March 1963), 80 p.
Evermann, Barton Warren, and Edmund Lee Goldsborough.
1907. The fishes of Alaska. Bull. Bur. Fish.Vol. 26, 1906, Bur. Fish. Doc.No. 624:219–360.
Fassett, H. C.
1902. The Karluk hatchery. *In* Alaska salmon investigations in 1900 and 1901, by J. F. Moser, p. 331–348. Bull. U.S. Fish Comm. 21:173–398.
Favorite, F., A. J. Dodimead, and K. Nasu.
1976. Oceanography of the subarctic Pacific Region, 1960–71. Int. North Pac. Fish. Comm., Bull. No. 33, 187 p.
Feuer, Robert C.
1958. Mammals collected in the Karluk Lake region, Kodiak Island, Alaska. Murrelet 39(1):37–39.
Finney, Bruce P.
1998. Long-term variability of Alaska sockeye salmon abundance determined by analysis of sediment cores.

North Pac. Anadromous Fish Comm., Bull. No. 1:388-395.

Finney, Bruce P., Irene Gregory-Eaves, Jon Sweetman, Marianne S. V. Douglas, and John P. Smol.

2000. Impacts of climate change and fishing on Pacific salmon abundance over the past 300 years. Science 290:795–799.

Finney, Bruce P., Irene Gregory-Eaves, Marianne S. V. Douglas, and John P. Smol.

2002. Fisheries productivity in the northeastern Pacific Ocean over the past 2,200 years. Nature 118:729–733.

Foerster, R. E.

1934. An investigation of the life history and propagation of sockeye salmon (*Oncorhynchus nerka*) at Cultus Lake, British Columbia. No. 4. The life history cycle of the 1925 year class with natural propagation. Contrib. Can. Biol. Fish. 8:345–355.

1936. An investigation of the life history and propagation of sockeye salmon (*Oncorhynchus nerka*) at Cultus Lake, British Columbia. No. 5. The life history cycle of the 1926 year-class with artificial propagation involving the liberation of free-swimming fry. J. Biol. Board Can. 2:311–333.

1937. The return from the sea of sockeye salmon (*Oncorhynchus nerka*) with special reference to percentage survival, sex proportions and progress of migration. J. Biol. Board Can. 3:26–42.

1968. The sockeye salmon, *Oncorhynchus nerka*. Fish. Res. Board Can. Bull. 162, 422 p.

Foerster, R. E., and A. L. Pritchard.

1941. Observations on the relation of egg content to total length and weight in the sockeye salmon (*Oncorhynchus nerka*) and the pink salmon (*O. gorbuscha*). Trans. Royal Soc. Can., Section V, Vol. 35:51–60.

Foster, M. B.

2004. Kodiak Management Area salmon escapement and catch sampling results, 2003. Alaska Dep. Fish Game, Div. Commercial Fish., Reg. Info. Rep. No. 4K04-31 (July 2004), 110 p.

2005. Kodiak Management Area salmon escapement and catch sampling results, 2004. Alaska Dep. Fish Game, Div. Sport Fish and Commercial Fish., Fish. Manag. Rep. No. 05-47 (August 2005), 103 p.

Foster, M. Birch.

2006. Kodiak Management Area salmon escapement and catch sampling results, 2005. Alaska Dep. Fish Game, Div. Sport Fish and Commercial Fish., Fish. Manag. Rep. No. 06-38 (July 2006), 98 p.

2007. Kodiak Management Area salmon escapement and catch sampling results, 2006. Alaska Dep. Fish Game, Div. Sport Fish and Commercial Fish., Fish. Manag. Rep. No. 07-14 (April 2007), 91 p.

2008. Kodiak Management Area salmon escapement and catch sampling results, 2007. Alaska Dep. Fish Game, Div. Sport Fish and Commercial Fish., Fish. Manag. Rep. No. 08-37 (June 2008), 104 p.

2009. Kodiak management area salmon escapement and catch sampling results, 2008. Alaska Dep. Fish Game, Div. Sport Fish and Commercial Fish., Fish. Manag. Rep. No. 9-24 (June 2009), 100 p.

2010. Kodiak management area salmon escapement and catch sampling results, 2009. Alaska Dep. Fish Game, Div. Sport Fish and Commercial Fish., Fish. Manag. Rep. No. 10-28 (June 2010), 96 p.

2011. Kodiak management area salmon escapement and catch sampling results, 2010. Alaska Dep. Fish Game, Div. Sport Fish and Commercial Fish., Fish. Manag. Rep. No. 11-30 (May 2011), 97 p.

Foster, M. B., and Mark J. Witteveen

2003. Kodiak Management Area salmon escapement and catch sampling results, 2002. Alaska Dep. Fish Game, Div. Commercial Fish., Reg. Info. Rep. No. 4K03-43 (August 2003), 112 p.

French, R., H. Bilton, M. Osako, and A. Hartt.

1976. Distribution and origin of sockeye salmon (*Oncorhynchus nerka*) in offshore waters of the North Pacific Ocean. Int. North Pac. Fish. Comm., Bull. No. 34, 113 p.

Friedmann, Herbert.

1935a. Avian bones from prehistoric ruins on Kodiak Island, Alaska. J. Wash. Acad. Sci. 25(1):44–51.

1935b. The birds of Kodiak Island, Alaska. Bull. Chicago Acad. Sci. 5(3):13–54.

Fukuhara, F. M.

1971. An analysis of the biological and catch statistics of the Japanese mothership salmon fishery. Ph.D. thesis, 238 p. Univ. Wash., Seattle.

Gard, Richard.

1971. Brown bear predation on sockeye salmon at Karluk Lake, Alaska. J. Wildl. Manage. 35(2): 193–204.

1973. Travel time and influencing factors for migrating adult sockeye salmon in Karluk River, Alaska. Trans. Am. Fish. Soc. 102 (4):723–727.

Gard, Richard, and Benson Drucker.

1963. Red salmon studies at Karluk Lake, 1962. U.S. Dep. Fish Wildl. Serv., Bur. Commercial Fish., Auke Bay Biol. Lab., Manuscr. Rep. 1963, MR 63-7 (May 1963), 44 p.

1965. Red salmon studies at Karluk Lake, 1963. U.S. Dep. Fish Wildl. Serv., Bur. Commercial Fish., Auke Bay Biol. Lab., Manuscr. Rep. 1965, MR 65-2 (Apr. 1965), 50 p.

1966a. Red salmon studies at Karluk Lake, 1964. U.S. Dep. Fish Wildl. Serv., Bur. Commercial Fish., Auke Bay Biol. Lab., Manuscr. Rep. 1966, MR 66-1 (May 13, 1966), 34 p.

1966b. Red salmon studies at Karluk Lake, 1965. U.S. Dep. Fish Wildl. Serv., Bur. Commercial Fish., Auke Bay Biol. Lab., Manuscr. Rep. 1966, MR 66-3 (September 20, 1966), 45 p.

Gard, R., and B. Drucker.

1986. Catch and escapement patterns in the Karluk River system. Annu. Rep. School Fish. Sci., Univ. Alaska, Juneau, 1984–1985:9.

Gard, Richard, Benson Drucker, and Robert Fagen.

1987. Differentiation of subpopulations of sockeye salmon (*Oncorhynchus nerka*), Karluk River system,

Alaska. *In:* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management, H. D. Smith, L. Margolis, and C. C. Wood (eds.), p. 408–418. Can. Spec. Publ. Fish. Aquat. Sci. 96.

Gilbert, Charles H.

1922. Kamchatka sea eagle at Kodiak, Alaska. Condor 24:66.

Gilbert, Charles H., and Henry O'Malley.

1920. Special investigation of salmon fishery in central and western Alaska. *In* Alaska fisheries and fur industries in 1919, by Ward T. Bower, p. 143–160. Appendix IX to Rep. U.S. Comm. Fish. for 1919, Bur. Fish. Doc. No. 891.

Gilbert, Charles H., and Willis H. Rich.

1927. Investigations concerning the red-salmon runs to the Karluk River, Alaska. Bull. U.S. Bur. Fish., Vol. 43, Part 2, Doc. No. 1021, 69 p.

Godfrey, H.

1958. A comparison of sockeye salmon catches at Rivers Inlet and Skeena River, B. C., with particular reference to age at maturity. J. Fish. Res. Board Can. 15:331–354.

Godfrey, H., D. D. Worlund, and H. T. Bilton.

1968. Tests on the accuracy of ageing chinook salmon (*Oncorhynchus tshawytscha*) from their scales. J. Fish. Res. Board Can. 25:1971–1982.

Grantham, Anjuli.

2011. Fishing at Karluk: Nature, technology, and the creation of the Karluk Reservation in Territorial Alaska. MA thesis, 62 p. Univ. South Carolina, Columbia.

Greenbank, John.

1957. Aggregational behavior in a freshwater sculpin. Copeia 1957(2):157.

1966. Notes on the life history of the sculpin, *Cottus aleuticus* Gilbert, in Karluk Lake, Alaska. U.S. Dep. Fish Wildl. Serv., Bur. Commercial Fish., Auke Bay Biol. Lab., Manuscr. Rep.–File, MR-F 29 (March 1966), 22 p.

Greenbank, John, and Philip R. Nelson.

1959. Life history of the threespine stickleback *Gasterosteus aculeatus* Linnaeus in Karluk Lake and Bare Lake Kodiak Island, Alaska. U.S. Fish Wildl. Serv., Fish. Bull. 59(153):537–559.

Gregory-Eaves, Irene, John P. Smol, Marianne S. V. Douglas, and Bruce P. Finney.

2003. Diatoms and sockeye salmon (*Oncorhynchus nerka*) population dynamics: Reconstructions of salmon-derived nutrients over the past 2,200 years in two lakes from Kodiak Island, Alaska. J. Paleolimnol. 30(1):35–53.

Gretsch, Dennis, Kevin Brennan, and Dave Prokopowich.

1992. Kodiak Management Area annual finfish management report, 1991. Alaska Dep. Fish Game, Div. Commercial Fish., Reg. Info. Rep. 4K92-37 (Oct. 1992).

Grinnell, Joseph.

1901. Record of Alaskan birds in the collection of the Leland Stanford Junior University. The Condor 3:19–23.

Grogan, Frank.

1969. Bear-salmon study, Karluk Lake, 1953. U.S. Dep. Fish Wildl. Serv., Bur. Commercial Fish., Auke Bay Biol. Lab., Manuscr. Rep.–File, MR-F No. 71 (Oct. 1969) [Also Titled "1953 Summer Report"], 17 p.

Groot, C.

1965. On the orientation of young sockeye salmon (*Oncorhynchus nerka*) during their seaward migration out of lakes. Behaviour, Suppl. 14, 198 p.

1982. Modifications on a theme—a perspective on migratory behavior of Pacific salmon. *In* Proceedings of the Salmon and Trout Migratory Behavior Symposium, E. L. Brannon and E. O. Salo (eds.), p. 1–21. School Fish., Univ. Wash., Seattle.

Hartman, W. L., and R. L. Burgner.

1972. Limnology and fish ecology of sockeye salmon nursery lakes of the world. J. Fish. Res. Board Can. 29:699–715.

Hartman, W. L., W. R. Heard, and B. Drucker.

1967. Migratory behavior of sockeye salmon fry and smolts. J. Fish. Res. Board Can. 24(10):2069–2099.

Hartman, W. L., C. W. Strickland, and D. T. Hoopes.

1962. Survival and behavior of sockeye salmon fry migrating into Brooks Lake, Alaska. Trans. Am. Fish. Soc. 91:133–139.

Hartman, Wilbur L., and Charles Y. Conkle.

1960. Fecundity of red salmon at Brooks and Karluk lakes, Alaska. Fish. Bull. 61(180):53–60.

Hartman, Wilbur L., and Robert F. Raleigh.

1964. Tributary homing of sockeye salmon at Brooks and Karluk lakes, Alaska. J. Fish. Res. Board Can. 21(3):485–504.

Hartman, Wilbur L., Theodore R. Merrell, and Richard Painter.

1964. Mass spawning behavior of sockeye salmon in Brooks River, Alaska. Copeia 1964(2):362–368.

Hartt, A. C.

1966. Migrations of salmon in the North Pacific Ocean and Bearing Sea as determined by seining and tagging, 1959–1960. Int. North Pac. Fish. Comm., Bull. No. 19, 141 p.

Hartt, A. C., and M. B. Dell.

1986. Early oceanic migrations and growth of juvenile Pacific salmon. Int. North Pac. Fish. Comm., Bull. No. 46, 105 p.

Hasler, A. D., A. T. Scholz, and A. M. Horrall.

1978. Olfactory imprinting and homing in salmon. Am. Sci. 66:347–355.

Heard, W. R.

1964. Phototactic behavior of emerging sockeye salmon fry. Anim. Behav. 12:382–389.

Higgins, Elmer.

1938. Progress in biological inquiries, 1937. U.S. Dep. Commer., Bur. Fish., Admin. Rep. No. 30, Appendix I to Report of Commissioner of Fisheries for the fiscal year 1938.

1939. Progress in biological inquiries, 1938. U.S. Dep. Commer., Bur. Fish., Admin. Rep. No. 35, Appendix I to Report of Commissioner of Fisheries for the fiscal year 1939.

Hilliard, Douglas K.

1959a. Notes on the phytoplankton of Karluk Lake, Kodiak Island, Alaska. The Can. Field-Natural. 73(3):135–143.

1959b. The effects of low temperatures on larval cestodes and other helminths in fish. J. Parasitol. 45(3):291–294.
1960. Studies on the helminth fauna of Alaska. XXXVIII. The taxonomic significance of eggs and coracidia of some diphyllobothriid cestodes. J. Parasitol. 46:703–716.
1969. Studies on Chrysophyceae from some ponds and lakes in Alaska III. New or unusual chrysophytes from Pinguicula Lake, Kodiak Island, Alaska. *In* The Kodiak Island refugium: its geology, flora, fauna and history, T. N. V. Karlstrom and G. E. Ball (eds.), p. 104–120. The Boreal Institute, University of Alberta, Calgary. The Ryerson Press. 262 p.

Hoar, W. S.
1965. The endocrine system as a chemical link between the organism and its environment. Trans. Royal Soc. Can., Series 43:175–200.
1976. Smolt transformation: evolution, behavior, and physiology. J. Fish. Res. Board Can. 33:1234–1252.

Holland, J. S., and Marianne McKean (eds.).
1992. FRED 1991 Annual Report to the Alaska State Legislature. Alaska Dep. Fish Game, Div. Fish. Rehab., Enhance., and Dev., FRED Report Number 117 (Jan. 1992), 150 p.

Hoopes, David Townsend.
1962. Ecological distribution of spawning sockeye salmon in three lateral streams, Brooks Lake, Alaska. Ph.D. diss., 235 p. Iowa State University of Science and Technology, Ames.

Hubbs, Carl L.
1941. Predator control in relation to fish management in Alaska. American Wildlife Institute, Trans. of the Fifth North Am. Wildl. Conf. (March 18–20, 1940):153–162.

Hulten, Eric.
1940. History of botanical exploration in Alaska and Yukon territories from the time of their discovery to 1940. Botaniska Notiser 1940: 289–346.

Ito, J.
1964. Food and feeding habits of Pacific salmon (genus *Oncorhynchus*) in their oceanic life. Bulletin of the Nokka Hokkaido Reg. Fisheries Laboratory 29:85–97. (Transl. from Japanese; Fish. Res. Board Can., Transl. Ser. No. 1309)

Jackson, James, Joe Dinnocenzo, and Geoff Spalinger.
2010. Kodiak Management Area commercial salmon fishery annual management report, 2010. Alaska Dep. Univ. Alaska, Fish Game, Fish. Manage. Rep. No. 10-47 (December 2010), 184 p.

Jennings, Mark R.
1987. Faces from the past: Frederic Morton Chamberlain (1867–1921), pioneer fishery biologist of the American West. Fisheries 12(6):22–29.
1997. Barton Warren Evermann (1853–1932) and his contributions to North American ichthyology. *In* Collection building in ichthyology and herpetology, Theodore W. Pietsch and William D. Anderson, Jr. (eds.), p. 291–310. Am. Soc. Ichthyol. Herpetol., Spec. Publi. No. 3, 593 p. Allen Press Inc., Lawrence, KS.

Jones, E. Lester.
1915. Report of Alaska investigations in 1914 (December 31, 1914), 155 p. U. S. Dep. Commer., Bur. Fish., Govt. Print. Off., Washington, DC.

Jordan, David Starr.
1903. The parent-stream theory of the return of salmon. The Popular Science Monthly (Nov.) 64:48–52.

Jordan, David Starr, and Barton Warren Evermann.
1904. Preliminary report of the Alaska Salmon Commission. 58th Congr., 2d Sess., House of Rep., Doc. No. 477:3–37.

Juday, Chancey.
1916. Limnological apparatus. Trans. Wisconsin Acad. Sci., Arts, and Letters 18(2):566–592.

Juday, C., Willis H. Rich, G. I. Kemmerer, and Albert Mann.
1932. Limnological studies of Karluk Lake, Alaska, 1926–1930. U.S. Bur. Fish. Bull. 47(12):407–436.

Karlstrom, Thor N. V., and George E. Ball (eds.).
1969. The Kodiak Island refugium: its geology, flora, fauna and history, 262 p. The Boreal Institute, Univ. Alberta, Calgary. The Ryerson Press.

Kerns, O. E., Jr.
1961. Abundance and age of Kvichak River red salmon smolts. Fish. Bull. 61(189):301–320.

Khlebnikov, Kiril Timofeevich.
1994. Notes on Russian America. Parts II–V: Kad'iak, Unalashka, Atkha, the Pribylovs. Richard Pierce (ed.), Alaska History No. 42, The Limestone Press, Kingston, Ontario.

Kline, Thomas C., Jr.
1991. The significance of marine-derived biogenic nitrogen in anadromous Pacific salmon freshwater food webs. Ph.D. thesis, 114 p. Univ. Alaska, Fairbanks.
1992. Nitrogen isotope technique provides direct evidence for fertilization of sockeye nursery lakes by salmon carcasses. Univ. Alaska, Fairbanks, School Fish. Ocean Sci., SFOS Highlights RH92-1 (Jan. 1992):1–4.
1993. Stable isotope ecology of Alaskan sockeye salmon lakes. *In* Diving for Science, John N. Heine and Nicole L. Crane (eds.), p. 89–94. Proceedings of the American Academy of Underwater Sciences, Thirteenth Annual Scientific Diving Symposium, Asilomar Conference Center, Pacific Grove, CA, 19–22 September 1993.
2003. Trophic level implications when using natural stable isotope abundance to determine effects of salmon-derived nutrients on juvenile sockeye salmon ecology. *In* Nutrients in salmonid ecosystems: sustaining production and biodiversity, John G. Stockner (ed.), p. 229–236. Am. Fish. Soc., Symposium 34, Bethesda, MD.

Kline, Thomas C., and J. J. Goering.
1993. Stable isotope analysis of juvenile sockeye salmon. Final Report RSA # RS1131076/EN1132116, 21 p. Inst. Mar. Sci., School of Fish. and Ocean Sci., Univ. Alaska, Fairbanks.

Kline, Thomas C., John J. Goering, Ole A. Mathisen, and Jeffery P. Koenings.
1990. Recycling of elements transported upstream by run of Pacific salmon (returns). *In* Research on Pacific

Salmon Biology, Mini-Symposium Abstracts, August 6, 1990, p. 10–11. Rep. No. AK-SG-90-08, Univ. Alaska, Juneau Center Fish. and Ocean Sci., Juneau, AK, and Alaska Sea Grant Program, Fairbanks.

Kline, Thomas C., Jr., John J. Goering, Ole A. Mathisen, Patrick H. Poe, Patrick L. Parker, and Richard S. Scalan.

1993. Recycling of elements transported upstream by runs of Pacific salmon: II. $\delta^{15}N$ and $\delta^{13}C$ evidence in the Kvichak River watershed, Bristol Bay, southwestern Alaska. Can. J. Fish. Aquat. Sci. 50:2350–2365.

Kline, Thomas C., Jr., John J. Goering, and Robert J. Piorkowski.

1997. The effect of salmon carcasses on Alaskan freshwaters. *In* Freshwaters of Alaska: Ecological syntheses, Alexander M. Milner and Mark W. Oswood (eds.), p. 179–204. Ecological Studies 119, Springer-Verlag, New York, NY, 369 p.

Knecht, Richard Arden.

1995. The late prehistory of the Alutiiq people: culture change on the Kodiak Archipeligo from 1200–1750 AD. Ph.D. thesis, 771 p. Bryn Mawr College, Bryn Mawr, PA.

Knecht, Richard A., and Richard H. Jordan.

1985. Nunakakhnak: an historic period Koniag village in Karluk, Kodiak Island, Alaska. Arctic Anthropol. 22(2):17–35.

Kociolek, John P., and Bruno de Reviers.

1996. The diatom types of Emile Manguin. I. Validating descriptions and designation of iconotypes for the Lake Karluk species. Cryptogamie: Algologie 17:175–191.

Koenings, J. P., and R. D. Burkett.

1987a. Population characteristics of sockeye salmon (*Oncorhynchus nerka*) smolts relative to temperature regimes, euphotic volume, fry density, and forage base within Alaskan lakes. *In* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management, H. D. Smith, L. Margolis, and C. C. Wood (eds.), p. 216–234. Can. Spec. Publ. Fish. and Aquat. Sci. 96.

1987b. An aquatic Rubic's cube: Restoration of the Karluk Lake sockeye salmon (*Oncorhynchus nerka*). *In* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management, H. D. Smith, L. Margolis, and C. C. Wood (eds.), p. 419–434. Can. Spec. Publ. Fish. and Aquat. Sci. 96.

1988. Karluk Lake sockeye salmon investigations. Section B : Limnological trends at Karluk Lake, Alaska, 1985–1987. Alaska Dep. Fish Game, Div. Fish. Rehab., Enhance., and Dev., Federal Aid in Anadromous Fish Conservation Project (1 July 1987–30 June 1988), Proj. AFS-52, Segment 3 (Dec. 1988), 23 p.

Koenings, J. P., Jim A. Edmundson, Gary B. Kyle, and John M. Edmundson.

1987. Limnology field and laboratory manual: methods for assessing aquatic production. Alaska Dep. Fish Game, Div. Fish. Rehab., Enhance., and Dev., FRED Rep. No. 71 (Feb. 1987), 212 p.

Konovalov, S. M.

1975. Differentiation of local populations of sockeye salmon *Oncorhynchus nerka* (Walbaum). Univ. Wash., Publ. Fish., New Ser. 6, 290 p.

Kovel, Ralph and Terry.

1998. The label made me buy it: From Aunt Jemima to Zonkers – The best-dressed boxes, bottles, and cans from the past. Crown Publishers, Inc., New York, NY. 214 p.

Krümmel, E. M., R. W. Macdonald, L. E. Kimpe, I. Gregory-Eaves, M. J. Demers, J. P. Smol, B. Finney, and J. M. Blais.

2003. Delivery of pollutants by spawning salmon. Nature 425:255–256.

Kuriscak, Paul.

2004. Kodiak Management Area salmon escapement daily cumulative counts for fish-weirs, 1993–2002. Alaska Dep. Fish Game, Div. Commercial Fish., Reg. Info. Rep. No. 4K04-38 (August, 2004), 260 p.

Kutchin, Howard M.

1899. Report on the salmon fisheries of Alaska, 1898. U.S. Treasury Dep., Office of Special Agent, Doc. No. 2095, 61 p.

1901. Report on the salmon fisheries of Alaska, 1900. U.S. Treasury Dep., Office of Special Agent, 56th Congress, 2d Session, Senate Doc. No. 168, 85 p.

1902. Report on the salmon fisheries of Alaska, 1901. U.S. Treasury Dep., Office of Special Agent, 57th Congress, 1st Session, Senate Doc. No. 138, 95 p.

1903. Report on the salmon fisheries of Alaska, 1902. U.S. Treasury Dep., Office of Special Agent, 57th Congress, 2d Session, Senate Doc. No. 113, 63 p.

1904. Report on the salmon fisheries of Alaska, 1903. U.S. Dep. Commerce and Labor, Office of Special Agent at Alaska Salmon Fisheries, Doc. No. 12, 47 p.

1905. Report on the salmon fisheries of Alaska, 1904. U.S. Dep. Commerce and Labor, Div. of Alaskan Fish., Doc. No. 35, 49 p.

1906. Report on the salmon fisheries of Alaska, 1905. U.S. Dep. Commerce and Labor, Div. of Alaskan Fish., Doc. No. 53, 32 p.

Kyle, G. B.

1990. Summary of acoustically-derived population estimates and distributions of juvenile sockeye salmon (*Oncorhynchus nerka*) in 17 lakes of southcentral Alaska, 1982–1987. Alaska Dep. Fish Game, Div. Fish. Rehab., Enhance., and Dev., FRED Report Number 104 (June 1990), 47 p.

Lander, A. H., and G. K. Tanonaka.

1964. Marine growth of western Alaskan sockeye salmon (*Oncorhynchus nerka* Walbaum). Int. North Pac. Fish. Comm., Bull. No. 14:1–31.

Le Brasseur, R. J.

1966. Stomach contents of salmon and steelhead trout in the northeastern Pacific Ocean. J. Fish. Res. Board Can. 23:85–100.

Lindsley, Roy R.

1978. How I killed the world's largest bear. Alaska Magazine 44(1):A26–A30 (Alaska-Yukon section).

Lisiansky, Urey.

1814. A Voyage Round the World in the Years 1803, 4, 5, and 6, Performed by Order of His Imperial Majesty Alexander the First, Emperor of Russia in the Ship *Neva*, 388 p. London: Printed for J. Booth.

Luttrell, Paul S.
1898. Report of Special Agent Luttrell for the year 1893. Condensation and rearrangement of data embodied in Annual Report of Paul S. Luttrell, Special Agent for the Salmon Fisheries in Alaska, year 1893. *In* Salmon Fisheries of Alaska, Reports of Special Agents Pracht, Luttrell, and Murray for the years 1892, 1893, 1894, 1895, p. 397–403. Seal and Salmon Fisheries and General Resources of Alaska, Volume II, Govt. Print. Off., Washington, DC.

Machidori, S.
1966. Vertical distribution of salmon (genus *Oncorhynchus*) in the northwestern Pacific. Bull. Hokkaido Reg. Fish. Res. Lab. 31:11–17. (Transl. from Japanese; U.S. Joint Publ. Res. Serv.; available at Alaska Fisheries Science Center, Seattle, WA)

Malloy, Larry.
1988. Interception of Cook Inlet-bound sockeye in the 1988 Kodiak commercial salmon fishery. An in-season management perspective. Alaska Dep. Fish Game, Div. Commercial Fish., Reg. Info. Rep. 4K88-7 (December, 1988), 40 p.

Malloy, Lawrence M., and David L. Prokopowich.
1992. Kodiak Management Area annual finfish management report, 1988. Alaska Dep. Fish Game, Div. Commercial Fish., Reg. Info. Rep. 4K92-7 (Feb. 1992), 269 p.

Manguin, Emile.
1960. Contribution a la flore diatomique de l'Alaska: Lac Karluk, especes critiques ou nouvelles. Revue algologique, N.S., 5(4):266–288.

Mannix, Daniel P.
1947. King of the flesh eaters. True, The Man's Magazine. Dec. 1947:40–43, 142–149.

Manzer, J. I.
1964. Preliminary observation on the vertical distribution of Pacific salmon (genus *Oncorhynchus*) in the Gulf of Alaska. J. Fish. Res. Board Can. 21:891–903.

Marr, J. C.
1957. The problem of defining and recognizing subpopulations of fishes. *In* Contributions to the study of subpopulations of fishes, J. C. Marr (coordinator). U.S. Dep. Fish Wildl. Serv., SSRF 208:1–6.

Marsh, Millard C., and John N. Cobb.
1908. The fisheries of Alaska in 1907. U.S. Dep. Commerce and Labor, Bur. Fish., Doc. No. 632.
1911. The fisheries of Alaska in 1910. U.S. Dep. Commerce and Labor, Bur. Fish., Doc. No. 746.

Martinson, Ellen C.
2004. Influence of three North Pacific Ocean regime shifts on the early marine growth and survival of sockeye salmon *Oncorhynchus nerka* from Karluk Lake, Alaska. MS thesis, 152 p. Univ. Idaho, Moscow.

Martinson, Ellen C., John H. Helle, Dennis L. Scarnecchia, and Houston H. Stokes.
2008. Density-dependent growth of Alaska sockeye salmon in relation to climate–oceanic regimes, population abundance, and body size, 1925 to 1998. Mar. Ecol. Progr. Ser. 370:1–18.
2009a. Alaska sockeye salmon scale patterns as indicators of climatic and oceanic shifts in the North Pacific Ocean, 1922–2000. North Pacific Anadromous Fish Commission Bulletin 5:177–182. (Available at: http://www.npafc.org/new/publications/Bulletin/Bulletin%20No.%205/NPAFC_Bull_5_177-182(Martinson).pdf; accessed 28 July 2011)
2009b. Growth and survival of sockeye salmon (*Oncorhynchus nerka*) from Karluk Lake and River, Alaska, in relation to climatic and oceanic regimes and indices, 1922–2000. Fish. Bull. 107:488–500.

Mathisen, O. A.
1962. The effect of altered sex ratios on the spawning of red salmon. *In* Studies of Alaska red salmon, T. S. Y. Koo (ed.), p. 137–248. Univ. Wash. Publ. Fish., New Ser. 1, 449 p.

Mayr, E.
1963. Animal species and evolution, 797 p. Harvard University Press, Cambridge, MA.

McAlister, W. B., W. J. Ingraham, Jr., D. Day, and J. Larrance.
1969. Investigations by the United States for the International North Pacific Fisheries Commission—1967: oceanography. Int. North Pac. Fish. Comm. Annu. Rep. 1967:97–107.

McDonald, Marshall.
1889. Communications from Commissioner Marshall McDonald (Appendix B). *In* Investigation of the fur-seal and other fisheries of Alaska, Report from the Committee on Merchant Marine and Fisheries of the House of Representatives, Govt. Print. Off., Washington, DC.
1894. Report on the salmon fisheries of Alaska. Bull. U.S. Fish Comm., Vol. 12, for 1892:1–49. The Miscellaneous Documents (No. 122) of the House of Representatives for the Second Session of the Fifty-Third Congress, 1893–1894. Vol. 18.

McGregor, Richard C.
1901. New Alaskan birds. The Condor 3:8.

McIntyre, John D. Reginald R. Reisenbichler, John M. Emlen, Richard L. Wilmot, and James E. Finn.
1988. Predation of Karluk River sockeye salmon by coho salmon and char. Fish. Bull. 86(3):611–616.

McKeown, Martha Ferguson.
1960. The trail led north. Mont Hawthorne's story, 222 p. Binfords and Mort, Publishers, Portland, OR.

McNair, Marianne, and J. S. Holland (eds.).
1993. FRED 1992 Annual Report to the Alaska State Legislature. Alaska Dep. Fish Game, Div. Fish. Rehab., Enhance. and Dev., FRED Rep. No. 127 (Jan. 1993), 102 p.

McPhail, J. D.
1961. A systematic study of the *Salvelinus alpinus* complex in North America. J. Fish. Res. Board Can. 18(5):793–816.

Meacham, C. P., and J. H. Clark.
1979. Management to increase anadromous salmon production. *In* Predator-prey systems in fisheries management, H. Clepper (ed.), p. 377–386. Sport Fishing Institute, Washington, DC.

Moore, J. Percy, and Marvin C. Meyer.
1951. Leeches (Hirudinea) from Alaskan and adjacent waters. The Wasmann J. Biol. 9(1):11–77.
Morton, William Markham.
1942. The ecology of two Alaskan charrs as shown by their parasites. MS thesis, 31 p. Univ. Wash., Seattle.
1975. The Dolly Varden is innocent. Alaska 41(5):14–15, 62–63.
1980. A collection of thumbnail autobiographies of former Pacific fisheries biologists I have known (15 December 1980). Pacific Fishery Biologist Memoirs, II–More Montlake Fishery Biologists in Review, 1(2):1–89.
1982. Comparative catches and food habits of Dolly Varden and arctic charrs, *Salvelinus malma* and *Salvelinus alpinus*, at Karluk, Alaska, in 1939–1941. Env. Biol. Fishes 7(1):7–28.
Moser, Jefferson F.
1899. The salmon and salmon fisheries of Alaska. Report of the operations of the U.S. Fish Commission steamer *Albatross* for the year ending June 30, 1898. Bull. U.S. Fish Comm., Vol. 18, for 1898:1–178.
1902. Salmon investigations of the steamer *Albatross* in the summer of 1900. Bull. U.S. Fish Comm., Vol. 21, for 1901:173–398.
Moyle, P.
1966. Feeding behavior of the Glaucous-winged gull on an Alaskan stream. Wilson Bull. 78:175–190.
Murray, John B., and Frank Van Hulle.
1974. Inventory and cataloging of the sport fish and sport fish waters in Southwest Alaska. Alaska Dep. Fish Game, Div. Sport Fish, Federal Aid in Fish Restoration, Annual Performance Report (July 1, 1973 to June 30, 1974), Proj. F-9-6, Job G-1-B, Volume 15:1–21.
1979. Inventory and cataloging of the sport fish and sport fish waters in Southwestern Alaska. Alaska Dep. Fish Game, Div. Sport Fish, Federal Aid in Fish Restoration, Annual Performance Report (July 1, 1978 to June 30, 1979), Project F-9-11, Job G-1-B, Volume 20:1–47.
Murray, Joseph.
1896. Report on the salmon fisheries in Alaska, 1894, 34 p. U.S. Treasury Dep., Office of Special Agent, Govt. Print. Off., Washington, DC. (Note: This report was republished in 1898 as Report of Special Agent Murray on the salmon fisheries in Alaska for the year 1894. *In* Salmon Fisheries of Alaska, Reports of Special Agents Pracht, Luttrell, and Murray for the years 1892, 1893, 1894, 1895 p. 404–435. Seal and Salmon Fisheries and General Resources of Alaska, Volume II, Govt. Print. Off., Washington, DC.).
Naiman, Robert J., Robert E. Bilby, Daniel E. Schindler, and James M. Helfield.
2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. Ecosystems 5:399–417.
Neave, F.
1964. Ocean migrations of Pacific salmon. J. Fish. Res. Board Can. 21:1227–1244.
Needham, James G., and J. T. Lloyd.
1916. The life of inland waters, 438 p. Comstock Publ. Co., Ithaca, NY.
Nelson, Patricia A., and Charles O. Swanton.
1996. Summary of salmon catch, estimated escapement, and run numbers, and biological attributes of selected salmon catches and escapements, Kodiak Management Area, 1995. Alaska Dep. Fish Game, Commercial Fish. Manage. and Dev. Div., Reg. Info. Rep. No. 4K96-40 (Aug. 1996), 161 p.
Nelson, Patricia A., Mark J. Witteveen, Steve G. Honnold, Ivan Vining, and James J. Hasbrouck.
2005. Review of salmon escapement goals in the Kodiak Management Area. Alaska Dep. Fish Game, Fish. Manuscr. No. 05-05 (Sept. 2005), 333 p.
Nelson, Philip R.
1958. Relationship between rate of photosynthesis and growth of juvenile red salmon. Science 128(3317):205–206.
1959. Effects of fertilizing Bare Lake, Alaska, on growth and production of red salmon (*O. nerka*). Fish. Bull. 60(159):59–86.
Nelson, Philip R., and Carl E. Abegglen.
1955. Survival and spawning of gill-net-marked red salmon. U.S. Dep. Fish Wildl. Serv., Res. Rep. 40, 19 p.
Nelson, Philip R., and W. T. Edmondson.
1955. Limnological effects of fertilizing Bare Lake, Alaska. U.S. Dep. Fish Wildl. Serv., Fish. Bull. 56(102):415–436.
Nelson, Philip R., Richard F. Shuman, Webster K. Clark, and Russell R. Hoffman.
1963. Brown bear predation on spawning salmon, 1948–1953, Kodiak Island, Alaska. U.S. Dep. Fish Wildl. Serv., Bur. Commercial Fish., Auke Bay Biol. Lab., Manuscr. Rep.–File, MR-F 5 (July 1963), 29 p.
Nelson, Robert E., and Richard H. Jordan.
1988. A postglacial pollen record from western Kodiak Island, Alaska. Arctic 41(1):59–63.
Owen, John B., Charles Y. Conkle, and Robert F. Raleigh.
1962. Factors possibly affecting production of sockeye salmon in Karluk River, Alaska. U.S. Dep. Int., Fish Wildl. Serv., Bur. Commercial Fish., Biol. Lab., Auke Bay, AK, Manuscr. Rep. 1962, MR 62-8 (Aug. 1962), 57 p.
Pella, J. J.
1968. Distribution and growth of sockeye salmon fry in Lake Aleknagik, Alaska, during the summer of 1962. *In* Further studies of Alaska sockeye salmon, R. L. Burgner (ed.), p. 45–111. Univ. Wash. Publ. Fish., New Ser. 3.
Petroff, Ivan.
1884. Report on the population, industries, and resources of Alaska. U.S. Dep. Int., Census Office, Vol. 8, 10th Census, 189 p. (Note: Petroff's report was republished in 1898 in Seal and Salmon Fisheries and General Resources of Alaska, Volume IV, Govt. Print. Off., Washington, DC.)
Pierce, Richard A. (ed.).
1978. The Russian Orthodox religious mission in America, 1794–1837, with material concerning the life

and works of the Monk German, and ethnographic notes by the Hieromonk Gedeon. Translated by Colin Bearne. Materials for the Study of Alaska History No. 11, 186 p. The Limestone Press, Kingston, Ontario.

1980. Siberia and Northwestern America, 1788–1792. The journal of Carl Heinrich Merck, Naturalist with the Russian Scientific Expedition led by Captains Joseph Billings and Gavriil Sarychev. Translated by Fritz Jaensch. Materials for the Study of Alaska History No. 17, 215 p. The Limestone Press, Kingston, Ontario.

Pietsch, Theodore W., and J. Richard Dunn.

1997. Early collection building in Puget Sound and adjacent waters: The 1880 expedition of David Starr Jordan (1851–1931) and Charles Henry Gilbert (1859–1928). *In* Collection building in ichthyology and herpetology, Theodore W. Pietsch and William D. Anderson, Jr. (eds.), p. 279–290. Am. Soc. Ichthyol. Herpetol., Spec. Publ. No. 3, 593 p. Allen Press Inc., Lawrence, KS.

Piper, C. V.

1905. Report of C. V. Piper on the grazing lands of the south Alaska coast and their possible utilization. *In* U.S. Department of Agriculture, Annual Report of the Office of Experiment Stations for the year ended June 30, 1904, p. 269–285. Govt. Print. Off., Washington, DC.

Porter, Robert P.

1893. Report on population and resources of Alaska at the Eleventh Census: 1890. U.S. Dep. Int., Census Office, Vol. 8, Govt. Print. Off., Washington, DC, 282 p.

Pracht, Max.

1898. Report of Special Agent Pracht for the year 1892. *In* Salmon Fisheries of Alaska, Reports of Special Agents Pracht, Luttrell, and Murray for the years 1892, 1893, 1894, 1895, p. 385–396. Seal and Salmon Fisheries and General Resources of Alaska, Vol. II, Govt. Print. Off., Washington, DC.

Prokopowich, Dave L.

2000. Kodiak Management Area commercial salmon annual management report, 1998. Alaska Dep. Fish Game, Div. Commercial Fish., Reg. Info. Rep. No. 4K00-2.

Prokopowich, Dave, Kevin Brennan, and Dennis Gretsch.

1998. Kodiak area commercial salmon fishery harvest strategy, 1998. Alaska Dep. Fish Game, Commercial Fish. Manage. Dev. Div., Reg. Info. Rep. No. 4K98-26 (May 1998), 54 p.

Quinn, T. P.

1980. Evidence for celestial and magnetic compass orientation in lake migrating sockeye salmon fry. J. Compar. Physiol. 137:243–248.

1982a. Intra-specific differences in sockeye salmon fry compass mechanisms. *In* Proceedings of the Salmon and Trout Migratory Behavior Symposium, E. L. Brannon and E. O. Salo (eds.), p. 79–111. School Fish., Univ. Wash., Seattle.

1982b. A model for salmon navigation on the high seas. *In:* Proceedings of the Salmon and Trout Migratory Behavior Symposium, E. L. Brannon and E. O. Salo (eds.), p. 229–237. School Fish., Univ. Wash., Seattle.

Quinn, T. P., and E. L. Brannon.

1982. The use of celestial and magnetic cues by orienting sockeye salmon smolts. J. Compar. Physiol. 147:547–552.

Raleigh, Robert F.

1960. The composition, abundance, and depth distribution of the 1957 summer net zooplankton of Bare Lake, Alaska. MS thesis, 30 p. Utah State Univ., Logan.

1963. The composition, abundance, and depth distribution of the 1957 summer net zooplankton of Bare Lake, Alaska, after fertilization. U.S. Fish Wildl. Serv., SSRF No. 423. 14 p.

1967. Genetic control in the lakeward migrations of sockeye salmon (*Oncorhynchus nerka*) fry. J. Fish. Res. Board Can. 24(12):2613–2622.

1969. Genetic control in lakeward migrations of sockeye salmon (*Oncorhynchus nerka*) fry. Ph.D. diss., 66 p. Univ. Idaho.

Rausch, Robert.

1954. Studies on the helminth fauna of Alaska. XXI. Taxonomy, morphological variation, and ecology of *Diphyllobothrium ursi* n. sp. provis. on Kodiak Island. J. Parasitol. 40:540–563.

Rich, Willis H.

1963. Notes from the diary of Willis H. Rich 1922–1933. U.S. Fish Wildl. Serv., Bur. Commercial Fish., Auke Bay Biol. Lab., Manuscr. Rep.–File, MR-F No. 1.

Rich, Willis H., and Edward M. Ball.

1931. Statistical review of the Alaska salmon fisheries, Part II: Chignik to Resurrection Bay. Bull. U.S. Bur. Fish., Vol. 46, 1930, Bur. Fish. Doc. No. 1102:643–712.

Rich, Willis H., and Frederick G. Morton.

1930. Salmon-tagging experiments in Alaska, 1927 and 1928. Bull. U.S. Bur. Fish., Vol. 45, 1929, Bur. Fish. Doc. No. 1057:1–23.

Ricker, W. E.

1982. Size and age of British Columbia sockeye salmon (*Oncorhynchus nerka*). Can. Fish. Aquat. Sci., Tech. Rep. No. 1115, 32 p.

Ricker, W. E., and H. D. Smith.

1975. A revised interpretation of the history of the Skeena River sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 32:1369–1381.

Ricker, William E.

1933. Destruction of sockeye salmon by predatory fishes. Biol. Board Can., Pac. Prog. Rep., No. 18:3–4.

1959. Evidence for environmental and genetic influence on certain characters which distinguish stocks of the Pacific salmons and steelhead trout. Fish. Res. Board Can., M.S. Rep. 695:1–103.

1962. Comparison of ocean growth and mortality of sockeye salmon during their last two years. J. Fish. Res. Board Can. 19(4):531–560.

1972. Hereditary and environmental factors affecting certain salmonid populations. *In* The stock concept in Pacific salmon, Raymond C. Simon and Peter A.

Larkin (eds.), p. 19–160. H. R. MacMillan Lectures in Fisheries, Univ. British Columbia, Vancouver.
Rogers, D. E., L. Gilbertson, and D. Eggers.
1972. Predator-prey relationship between Arctic char and sockeye salmon smolts at the Agulowak River, Lake Aleknagik, in 1971. Univ. .Wash., Fish. Res. Inst., Circ. No. 72-7, 40 p.
Roos, John F.
1959. Feeding habits of the Dolly Varden, *Salvelinus malma* (Walbaum), at Chignik, Alaska. Trans. Am. Fish. Soc. 88(4):253–260.
Roosevelt, Theodore.
1904. Alaska Salmon Commission. Message from the President of the United States, transmitting a communication from the Secretary of Commerce and Labor submitting a preliminary report of the Alaska Salmon Commission. 58th Congress, Second Session, House of Representatives, Doc. No. 477:1–3.
Roppel, Patricia.
1982. Alaska's salmon hatcheries, 1891–1959. Alaska Historical Commission Studies in History No. 20, Natl. Mar. Fish. Serv., Auke Bay Fish. Lab., 299 p.
1986. Salmon from Kodiak: an history of the salmon fishery of Kodiak Island, Alaska. Alaska Historical Commission Studies in History No. 216, 355 p.
Rounsefell, George A.
1957. Fecundity of North American Salmonidae. Fish. Bull. 57(122):451–468.
1958. Factors causing decline in sockeye salmon of Karluk River, Alaska. Fish. Bull. 58(130): 83–169.
1973. Comments on "Evaluation of causes for the decline of the Karluk sockeye salmon runs and recommendations for rehabilitation," by R. Van Cleve and D. E. Bevan. Fish. Bull. 71(3):651–659.
1977. No Title (Memorial to George A. Rounsefell). Northeast Gulf Science 1(1):1–7.
Rutter, Cloudsley.
1899. Notes on a collection of tide-pool fishes from Kadiak Island in Alaska. Bull. U.S. Fish Comm., Vol. 18 (for 1898):189–192.
1903a. Natural history of the quinnat salmon. A report of investigations in the Sacramento River, 1896–1901. Bull. U.S. Fish Comm., Vol. 22 (for 1902):65–141.
1903b. The eagles of Karluk Lake. Western Field 3(4):671–674.
1903c. The Pacific salmons. Country Life in America 4 (June 1903):124–127.
Schmidt, D. C., G. B. Kyle, S. R. Carlson, H. J. Geiger, and B. Finney.
1997. Alaska's sockeye salmon fishery management: can we learn from success? *In* Developing and Sustaining World Fisheries Resources: The State of Science and Management, D. A. Hancock, D. C. Sminth, A. Grant, and J. P. Beumerm (eds.), p. 687–695. Second World Fisheries Congress Proceedings, CSIRO, Collingwood, VIC, Australia.
Schmidt, Dana C., Stan R. Carlson, Gary B. Kyle, and Bruce P. Finney.
1998. Influence of carcass-derived nutrients on sockeye salmon productivity of Karluk Lake, Alaska: Importance in the assessment of an escapement goal. North Am. J. Fish. Manage. 18(4):743–763.
Schrof, Stephen T., and Steven G. Honnold.
2003. Salmon enhancement, rehabilitation, evaluation, and monitoring efforts conducted in the Kodiak Management Area through 2001. Alaska Dep. Fish Game, Div. Commercial Fish., Reg. Info. Rep. No. 4K03-41.
Schrof, Stephen T., Steven G. Honnold, Christian J. Hicks, and Jeff A. Wadle.
2000. A summary of salmon enhancement, rehabilitation, evaluation, and monitoring efforts conducted in the Kodiak Management Area through 1998. Alaska Dep. Fish Game, Div. Commercial Fish., Reg. Info. Rep. No. 4K00-57.
Seale, Alvin.
1898. Notes on Alaskan water birds. Proc. Acad. Natural Sci. Philadelphia 50:126–140.
Setchell, William Albert, and Nathaniel Lyon Gardner.
1903. Algae of northwestern America. Univ. Calif. Publ. Bot. 1:165–418.
Shuman, Richard F.
1950. Bear depredations on red salmon spawning populations in the Karluk River system, 1947. J. Wildl. Manage. 14(1):1–9.
Skud, Bernard E., and W. Harry Everhart.
1977. George A. Rounsefell. Fisheries (Feb. 1977): 35–36.
Smith, Douglas G.
2001. Systematics and distribution of the Recent Margaritiferidae. *In* Ecology and evolution of the freshwater mussels Unionoida, G. Bauer and K. Wächtler (eds.), p. 33–49. Ecological Studies 145, Springer-Verlag, Berlin.
Smith, O. R.
1947. Returns from natural spawning of cutthroat trout and eastern brook trout. Trans. Am. Fish. Soc. 74:281–296.
Smithsonian Institution.
1891. Annual Report of the Board of Regents of the Smithsonian Institution showing the operations, expenditures, and condition of the institution for the year ending June 30, 1889. Rep. Natl. Mus., Govt. Print. Off., Washington, D. C.
Spalinger, Geoff.
2006. Kodiak Management Area salmon daily and cumulative escapement counts for river systems with fish weirs, 1996–2005. Alaska Dep. Fish Game, Div. Sport Fish and Commercial Fish., Fish. Manage. Rep. No. 06-06 (March 2006), 144 p.
Steller, Georg Wilhelm.
2003. Steller's history of Kamchatka: Collected information concerning the history of Kamchatka, its peoples, their manners, names, lifestyle, and various customary practices, Marvin W. Falk (ed.), Margritt Engel and Karen Willmore (translators). Hist. Transl. Ser. Vol. 12, 298 p. Univ. Alaska Press, Fairbanks.
Stickney, Robert R.
1989. Flagship. A history of fisheries at the University of Washington, 153 p. Univ. Washington, School Fish., Publ. Fish. Kendall/Hunt Publ. Co., Dubuque, IA.

Stone, Livingston.
1894. A National Salmon Park. *In* Report on the salmon fisheries of Alaska, by M. McDonald, p. 14–19. Bull. U.S. Fish Comm. 12, for 1892. The Miscellaneous Documents (No. 122) of the House of Representatives for the Second Session of the Fifty-Third Congress, 1893–1894, Vol. 18. (Originally published 16 June 1892 in *Forest and Stream*).

Svärdson, G.
1949. Natural selection and egg number in fish. Rep. Inst. Freshwater Res. Drottningholm 29:115–122.

Sweetman, Jon N., and Bruce P. Finney.
2003. Differential responses of zooplankton populations (*Bosmina longirostris*) to fish predation and nutrient-loading in an introduced and a natural sockeye salmon nursery lake on Kodiak Island, Alaska, U.S.A. J. Paleolimnol. 30(2):183–193.

Taft, Alan C.
1930. The growth of salmon. *In* Contributions to Marine Biology, p. 253–259. Stanford Univ. Press, Stanford, CA. (Lectures and symposia of meeting of Western Society of Naturalist, December 20–21, 1929)

Taylor, John P.
1964. Eighteen months at the Karluk hatchery. Alaska Sportsman 30(1):36.

Terrell, Terry T.
1987. The diatom flora (Bacillariophyta) in Karluk Lake, Alaska as determined from sediment cores. Nova Hedwigia 45(3–4):415–422.

Thompson, Seton H.
1957. Alaska fishery and fur-seal industries, 1955. U.S. Dep. Int., Fish. Wildl. Serv., Stat. Dig. No. 40.

Thompson, W. F., and D. E. Bevan.
1955. A proposal for experimental regulation of the Karluk fishery. Univ. Wash., Fish. Res. Inst., Circ. No. 72 revised, Kodiak Island Memo. No. 13 (November 16, 1954, revised October 12, 1955), 10 p.

Thompson, William Francis.
1950. Some salmon research problems in Alaska. A talk prepared for the Meeting held by the National Research Council, on scientific research in Alaska, Alaska Science Conference, Nov. 9–11, 1950, Washington, DC. Univ. Wash., Fish. Res. Inst., Circ. No. 11, 20 p.
1951. An outline for salmon research in Alaska. A talk prepared for the Meeting of the International Council for the Exploration of the Sea at Amsterdam, October 1–9, 1951. Univ. Wash., Fish. Res. Inst., Circ. No. 18, 49 p.

Thompson, William F., Donald E. Bevan, and Fredrik V. Thorsteinson.
1954. The present regulatory quota system for Karluk and Chignik. Univ. Wash., Fish. Res. Inst., Circ. No. 71, Kodiak Island Memo. No. 12 (November 16, 1954), 4 p.

Tiernan, Aaron R.
2011. Kodiak Management Area weir descriptions and salmon escapement report, 2010. Alaska Dep. Fish Game, Div. Sport Fish and Commercial Fish., Fish. Manage. Rep. No. 11-08 (March 2011), 138 p.

Tikhmenev, P. A.
1978. A history of the Russian-American Company, 522 p. Univ. Wash. Press, Seattle.

Tingle, George R.
1897. Report on the salmon fisheries of Alaska, 1896. U.S. Treasury Dep., Div. Special Agents, Doc. No. 1925, 27 p.

Turner, L. M.
1886. Contributions to the natural history of Alaska. Results of investigations made chiefly in the Yukon District and the Aleutian Islands; conducted under the auspices of the Signal Service, United States Army, extending from May, 1874, to August, 1881. No. II, Arctic Series of Publications Issued in Connection with the Signal Service, U.S. Army, 226 p. Govt. Print. Off., Washington, DC.

U.S. Geological Survey.
1974–1982. Water resources data for Alaska. U.S. Geological Survey, Water Data Reports, Water Years 1974–1982 (issued annually).

U.S. Government Printing Office.
1897. Register of the United States Commission of Fish and Fisheries. July 15, 1897,7 p. U.S. Govt. Print. Off., Washington, DC.

U.S. Senate.
1912. Alaska fisheries. Hearings before the subcommittee of the committee on fisheries. U.S. Senate. Sixty-second Congress, second session on S. 5856, a bill to amend an act for the protection and regulation of the fisheries of Alaska. Government Printing Office, Washington, D.C.

Van Arsdale, W. W., and W. E. Gerber.
1904. Eighteenth Biennial Report of the State Board of Fish Commissioners of the State of California, for the years 1903–1904, 112 p. California State Printing, Sacramento.

Van Cleve, Richard, and Donald E. Bevan.
1973. Evaluation of causes for the decline of the Karluk sockeye salmon runs and recommendations for rehabilitation. Fish. Bull. 71(3): 627–649, 661–663.

Van Daele, Larry.
2003. The history of bears on the Kodiak Archipelago. Alaska Natural Hist. Assoc., Anchorage, 88 p.

Van Hulle, Frank, and John B. Murray.
1973. Inventory and cataloging of the sport fish and sport fish waters in Southwest Alaska. Alaska Dep. Fish Game, Div. Sport Fish, Federal Aid in Fish Restoration, Annu. Progr. Rep. (July 1, 1972 to June 30, 1973), Proj. F-9-5, Job G-1-B, Vol. 14:1–28.
1977. Inventory and cataloging of the sport fish and sport fish waters in Southwestern Alaska. Alaska Dep. Fish Game, Div. Sport Fish, Federal Aid in Fish Restoration, Annu. Perf. Rep. (July 1, 1976 to June 30, 1977), Proj. F-9-9, Job G-1-B, Vol. 18:1–27.
1978. Inventory and cataloging of the sport fish and sport fish waters in Southwestern Alaska. Alaska Dep. Fish Game, Div. Sport Fish, Federal Aid in Fish Restoration, Annu. Perf. Rep. (July 1, 1977 to June 30, 1978), Proj. F-9-10, Job G-1-B, Volume 19: 1–41.

Vegter, I. Hettie.
1983. Index Herbariorum, Part II (5), Collectors N-R. *In* Index Herbariorum, a guide to the location and contents of the world's public herbaria, Frans A. Stafleu (ed.). Bohn, Scheltema, and Holkema, Utrecht, Antwerp.
Vladykov, V. D.
1956. Fecundity of wild speckled trout (*Salvelinus fontinalis*) in Quebec lakes. J. Fish. Res. Board Can. 13:799–841.
Wadle, J.A.
2001. Kodiak Management Area commercial salmon annual management report, 2000. Alaska Dep. Fish Game, Div. Commercial Fish., Reg. Info. Rep. No. 4K01-40.
2004. Kodiak Management Area commercial salmon annual management report, 2002. Alaska Dep. Fish Game, Div. Commercial Fish., Reg. Info. Rep. 4K04-01.
2005. Kodiak Management Area commercial salmon annual management report, 2003. Alaska Dep. Fish Game, Div. Commercial Fish., Reg. Info. Rep. 4K05-1.
Wadle, J. A., and K. Brennan.
2001. Kodiak Management Area commercial salmon annual management report, 1999. Alaska Dep. Fish Game, Div. Commercial Fish., Reg. Info. Rep. No. 4K01-5.
Wedemeyer, G. A., R. L. Saunders, and W. C. Clarke.
1980. Environmental factors affecting smoltification and early marine survival of anadromous salmonids. Mar. Fish. Rev. 42(6):1–14.
White, L.E.
1985. Karluk Lake sockeye rehabilitation, 1984. Progress Report. Alaska Dep. Fish Game, Div. Fish. Rehab., Enhance., and Dev., Federal Aid in Anadromous Fish Conservation (April 1, 1984–March 31, 1985), Proj. AFS-52, Segment 1 (May 1985), 45 p.
1986. Sockeye salmon rehabilitation at Upper Thumb River, Karluk Lake, Alaska 1978 to 1984. Alaska Dep. Fish Game, Div. Fish. Rehab., Enhance., and Dev., Juneau, FRED Report Number 69 (Dec. 1986), 58 p.
1988a. Karluk Lake sockeye salmon investigations. Section A: Annual Report. Alaska Dep. Fish Game, Div. Fish. Rehab., Enhance., and Dev., Federal Aid in Anadromous Fish Conservation (1 July 1987–30 June 1988), Proj. AFS-52, Segment 3 (Dec. 1988), 37 p.
1988b. Karluk Lake sockeye salmon investigations. Section C: Successful rehabilitation of Upper Thumb River sockeye salmon stock. Alaska Dep. Fish Game, Div. Fish. Rehab., Enhance., and Dev., Federal Aid in Anadromous Fish Conservation (1 July 1987–30 June 1988), Proj. AFS-52, Segment 3 (Dec. 1988), 28 p.
Willson, Mary F., and Karl C. Halupka.
1995. Anadromous fish as keystone species in vertebrate communities. Conserv. Biol. 9(3):489–497.
Wilmot, Richard L., and Carl V. Burger.
1985. Genetic differences among populations of Alaskan sockeye salmon. Trans. Am. Fish. Soc. 114(2): 236–243.
Withler, F. C.
1952. Estimation of the size of the sockeye smolt run, Babine Lake, 1951. Fish. Res. Board Can., Pacific Progr. Rep. No. 91:17–19.
Witteveen, Mark J., M. B. Foster, Nicholas H. Sagalkin, Kenneth A. Bouwens, Robert T. Baer, and Steve Schrof.
2005. Westward Region salmon run reconstruction estimates for 2003 and 2004 forecasts. Alaska Dep. Fish Game, Div. Commercial Fish., Reg. Info. Rep. 4K05-2 (February, 2005), 102 p.
Woodworth, Jim.
1958. The Kodiak bear, 204 p. The Stackpole Company, Harrisburg, PA.

APPENDIX I

Gazetteer: Karluk Lake and River Landmarks

Alder Creek: Lateral creek on east shore of Karluk Lake 3 km north of Lower Thumb River.

Barabara Point: Land point on east shore of Karluk Lake 1.5 km northwest of O'Malley River.

Bare Lake: Small lake 25 km southwest of Karluk Lake that was experimentally fertilized by the FWS during 1950–56. Bare Lake discharges into Bare Creek, a tributary of the Ayakulik River.

Barnaby Mountain: Name used in 1937 by Thomas Barnaby (notebook) for the mountain south of Camp Island, but later officially named Mount Shuman on U.S. Geological Survey maps.

Barnaby Ridge: Mountain just south of the Portage and bordering the west bank of the Karluk River. This name was first given by FWS biologists William Morton and Allan DeLacy (Morton notebook, 17 May 1941) and continued to be used from the 1940s–1950s (Nelson 1950 notebook) to present time by fishery biologists and personnel of the Kodiak National Wildlife Refuge. It was known by various other names before 1941, including **Hungerford Mountain** or **River Ridge** (Rich 1926 notebook) and **Lookout Mountain** (Morton 1940 notebook).

Barnaby Lake: Small lake west of Barnaby Ridge that flows via a west bank tributary into the middle Karluk River. Karlstrom et al. (1969) called this **Pinguicula Lake**.

Big Bear Creek: Lateral creek on east shore of Karluk Lake between Cottonwood and Alder Creeks.

Boulder Point: Land point on east shore of Karluk Lake 0.8 km south of Cottonwood Creek.

Bluff Point: Land point on west shore of Karluk Lake 1.5 km south of Eagle Creek. Gilbert first used this name (1921 notebook).

Camp Island (also called **Thumb Island**)**:** Large island in the middle of Karluk Lake that biologists used as a base camp for their fisheries studies (since 1889) because of its central location and partial protection from bears. At first, biologists camped in tents or sheltered in a Native barabara, but in 1927 the USBF built a cabin on Camp Island and more facilities were added in later years.

Camp Point: Land point on Camp Island first named by Barnaby in the 1930s (1930–1937 notebooks).

Canyon Creek: Terminal tributary at south end of Karluk Lake, once flowing directly into the lake a short distance east of the O'Malley River mouth, but now entering the lower O'Malley River. Its channel changed course in 1928. Gilbert and Rich first named this creek in 1922 (notebooks). Gilbert originally called this **Head Creek** (1921 notebook).

Cape Karluk (Karluk Head): Prominent mountain escarpment 3 km west of Karluk Spit and fronting on Shelikof Strait.

Cascade Creek: Lateral creek on the west shore at south end of Karluk Lake. Gilbert and Rich first named this creek in 1922 (notebooks). Gilbert originally called this **Willow Creek** (1921 notebook).

Coffee Point: Prominent land point on the north shore of Karluk Lagoon 4 km upstream of Karluk Spit. Clinton Gurnee used this name on a 1903 map. Name not currently used.

Cold Creek: Small branch of Spring Creek located at north end of Karluk Lake 0.8 km east of the lake's outlet. Gilbert (1921 notebook), Barnaby (1944 map), and Bevan (1951 FRI unpublished report) used this name.

Cotoid Creek: Small lateral creek in the vicinity of Little Lagoon Creek first named by Barnaby (1931 notebook). Name not currently used.

Cottonwood Creek: Lateral creek on east shore of Karluk Lake 4 km north of Camp Island. Gilbert called this **Windy Creek** in 1921 and **Defeat Creek** in 1922 (notebooks).

Cottonwood Point: Land point on east shore of Karluk Lake near Cottonwood Creek. Gilbert called this **Windy Point** (1921 notebook).

Deep Hole: Name originally used for two locations in the Karluk River basin: 1) a name used by Gilbert (1922 notebook) and Nelson (1946 notebook) for a deeper than normal spot in the upper Karluk River where adult Chinook salmon congregated (also called the "King Hole"), located 3–5 km downstream from the lake's outlet; and 2) a name used by USBF biologist Fred R. Lucas in 1922 for an area at the east end of Karluk Lagoon having deeper than normal water.

Discovery Creek: A lateral creek at the northeast end of Karluk Lake named by Rich (1922 notebook) and possibly the same as Moraine Creek. Name not currently used.

Dreadnaught City (also called **Dreadnought City** and **Wamberg's**)**:** A homestead, apparently owned

by Mr. Wamberg, with three small cabins located at the west end of Larsen Bay at the ocean end of the Karluk River Portage trail. The USBF later leased or purchased this site to support their Karluk research program. During 1921–50, USBF and FWS personnel used these facilities to store supplies and a tractor and as temporary shelter while traveling to and from Karluk Lake and River. Gilbert identified this site as early as 1921 (notebook) and Rich showed its location on a sketch map of the Karluk region (notebook, 31 May 1929).

We have found only one person, FWS seasonal biologist Arthur Freeman, who remembers how Dreadnaught City got its name:

> [FWS seasonal biologist Arthur Freeman discussing his summer experiences at Karluk in 1947–1948] But there was another player, too, who didn't participate in the Karluk projects, but on many occasions served as a host and communication intermediary. That player was Archie Brunton, whom we knew as "Scottie". He had emigrated from Scotland to Kodiak at some time in the distant past. At Karluk our communication with our base at Kodiak (Village) was maintained by transmitting to radio KOT (Larsen Bay), operated by Scottie, who in turn could communicate with Kodiak. Our 1.5 watt forest service radio at Karluk had a range of 15 miles. It was Scottie who told me how Dreadnaught City got its name. There was a homesteader who build the cabin and the barn there, and may have had a cow or two because there was still hay in the barn long after the homesteader had gone. The homesteader, according to Scottie, often told of his intentions of digging a canal to connect Larsen Bay with the Karluk River, a canal so big that a ship as big as a "Dreadnaught" (an early version of a British battle ship) could navigate through the canal. Of course, the notion is so far-fetched that it makes no sense, until you understand that exaggeration is much a part of wilderness humor. So much for the version of "Dreadnaught City". [Freeman letter, 24 October 1998 to Richard L. Bottorff]

Dumbell Island: See **Gull Island**.

Eagle Creek: Small lateral creek on west shore of Karluk Lake 3 km north of Meadow Creek. Barnaby used this name in 1930 (notebook).

Eagle Point: Land point on west shore of Karluk Lake just south of Eagle Creek. Gilbert first used this name (1921 notebook), followed by Rich (1927 notebook).

East Fork of Upper Thumb River: East tributary branch of the Upper Thumb River that originates 10–11 km southeast of Thumb Lake. After joining the North Fork it forms the main Upper Thumb River that flows 0.8 km into the east end of Thumb Lake.

Egg Island: See Gull Island.

Egg Islet (see also **Tern Island** and **Murray Island**)**:** Rich used this name for the small island in O'Malley Lake (1926 notebook).

Falls Creek: Creek at the south end of Karluk Lake that flows into the upper O'Malley River just downstream of the O'Malley Lake outlet (Gilbert 1921–22 notebooks). There is evidence that Falls Creek has shifted its channel several times over the years, discharging either into O'Malley Lake or the upper O'Malley River. Apparently the channel shifted in 1927, but a major change occurred in September 1947, forcing the creek to enter O'Malley Lake. ADF biologists diverted Falls Creek back to its original channel in 1953 by building a low dike, but this washed out in a 1954 storm and the creek flowed into O'Malley Lake. Recent maps show that Falls Creek enters the upper O'Malley River. First named by Gilbert and Rich in 1922 (notebooks).

Fry Creek: Small creek flowing into the Karluk River 180 m downstream from Karluk Lake's outlet. First named by Barnaby in the 1930s (1930–37 notebooks), but this term is not currently used.

Grassy Point: Land point on west shore of Karluk Lake 3 km northwest of Camp Island. First named by Gilbert and Rich (1922 notebooks). Gilbert originally called this Halfway Point (1921 notebook).

Grassy Point Creek: Lateral creek on west shore of Karluk Lake 3 km northwest of Camp Island. First named by Gilbert and Rich (1922 notebooks). Gilbert originally called this Halfway Creek (1921 notebook).

Grove Point: Land point on east shore of Karluk Lake 0.8 km south of Moraine Creek (shown on FRI map).

Gull Creek: Lateral creek on east shore of Karluk Lake between Long and Barabara points. USBF biologist Seymour P. Smith used this name in 1927 (notebook) while surveying the salmon streams, being first attracted to the creek by its large number of gulls. Barnaby also used this name in 1930 (notebook). Name not currently used.

Gull Island (also called **Egg Island, Dumbell Island,** and **Outer Island**)**:** Small island in Karluk Lake just north of Camp Island. Rich called this **Outer Island** in 1922 (notebook) and then **Dumbell Island** in 1926–29 (notebooks) because of its unique shape. Barnaby also called it Dumbell Island in the 1930s. It was referred to as **Egg Island** and Gull Island in later years for its many nesting gulls.

Hale's Cove: Name used in honor of Senator Hale by Barnaby in 1934 (notebook) for a small beach embayment on the east shore of Karluk Lake somewhere north of Lower Thumb River. Name not currently used.

Halfway Creek: Lateral creek on west shore of Karluk Lake 2.5 km west of Camp Island. Gilbert called this **Cottonwood Creek** in 1921 (notebook).

Hungerford Mountain (see also **Barnaby Ridge**): Rich showed the location of Hungerford Mountain on a sketch map of the Karluk region (notebook, 31 May 1929) and Barnaby used the name in 1930 (notebook). Name not currently used.

Island Point: Prominent land point projecting into Karluk Lake just south of Camp Island.

Jackpot Cove: Beach cove on east shore of Karluk Lake 1.5 km south of Island Point. FRI fishery biologists used this name in the 1950s for the site where they successfully captured many juvenile sockeye in beach seines. Name not currently used.

Julia Foard Point: Land point on Shelikof Strait between Tanglefoot Bay and the Karluk River mouth. Named for the bark *Julia Foard* that was blown ashore and wrecked in rough seas on 27 May 1888.

Karluk (also **Kallut** (Alutiiq), **Kerluta, Karlack, Karlukskaia, Karlook, Karlutsk, Carlook**): Various historical spellings of Karluk. The name "Karluk" is derived from the Alutiiq word "iqalluk," a term used for fish.

Karluk Lagoon: Shallow tidally-influenced estuary comprising the lower 5 km of the Karluk River before it discharges into Shelikof Strait.

Karluk Lake: Large deep lake (19.6 km long, 3.1 km wide, 126 m maximum depth) on southwest Kodiak Island.

Karluk Portage: 1) Site on the Karluk River 3 km west of Larsen Bay, once used as a weir location for counting sockeye salmon and for taking steelhead eggs, and 2) the 3 km trail connecting Larsen Bay and the Karluk River.

Karluk River: Large river on southwest Kodiak Island discharging from Karluk Lake. It flows 40 km north and west and discharges into Shelikof Strait at Karluk Spit.

Karluk Spit: Narrow strand bar about 1 km long that separates Shelikof Strait and Karluk Lagoon. Karluk Spit was once the location of many canneries and intensive beach seining for sockeye salmon in the early fishery.

Karluk Village: Alutiiq community originally located near the northeast end of Karluk Spit ("Old Karluk") where the Karluk River discharged into Shelikof Strait. Old Russian maps identified the village near the mouth of the Karluk River as **Nunakakhnak** (sometimes spelled **Nunakakhvak**). A new village ("New Karluk") arose near the west end of Karluk Spit after the Karluk River changed its course sometime before 1850 and began discharging into the ocean at this new location. Karluk Village was moved inland (southeast) 1.5 km following a violent windstorm in 1978.

Katzinjammer Creek: Unofficial name for a north bank tributary to the Karluk River 2.5 km upstream of the lower weir site. Rich first used this name in 1929 and recorded it on a sketch map (notebook, 31 May 1929). Barnaby also used this name in the 1930s (notebooks). USBF weir foreman Ray S. Wood referred to it as **Northeast Harbor Creek** in 1928. Name not currently used.

Katzinjammer Lake: Unofficial name of the small lake at the head of Katzinjammer Creek. Barnaby used this name in 1933 (notebook). Name not currently used.

King Hole: Deep pool in the Karluk River between the lake's outlet and the Portage where adult Chinook ("king") salmon accumulate during their migration to spawning areas in the upper river. Name used by Nelson in 1949 (notebook, 28 August 1949).

Larsen Bay: 1) a narrow ocean bay that extends inland 8 km from Uyak Bay to within 3 km of the Karluk River, and 2) the small community that grew up around the Alaska Packers Association cannery at the east end of Larsen Bay. In 1903 Rutter and Spaulding called this **Larsen Inlet**.

Little Bear Creek: Lateral creek on east shore of Karluk Lake 2.5 km north of Camp Island.

Little Lagoon Creek: Lateral creek on east shore of Karluk Lake directly east of Camp Island.

Lookout Mountain: Name used by USBF employee Fred R. Lucas on a 1922 sketch map for a mountain on the lower Karluk River and southeast of the lower weir site. Morton used this name in 1940 for **Barnaby Ridge**. Name not currently used.

Long Point: Land point on east shore of Karluk Lake 3 km northwest of O'Malley River. Gilbert originally called this **Point-no-Point** (1921 notebook).

Long Point Creek: Small lateral creek on east shore of Karluk Lake 3 km northwest of O'Malley River.

Lower Thumb River: Short terminal river outlet of Thumb Lake that discharges into Karluk Lake southeast of Camp Island.

Meadow Creek: Lateral creek on west shore of Karluk Lake 4 km northwest of O'Malley River mouth. First named by Gilbert and Rich (1922 notebooks). Gilbert originally called this **Green Point Creek** (1921 notebook).

Meadow Point (also called **Green Point**): Land point

on west shore of Karluk Lake 0.4 km south of Meadow Creek. Gilbert first used these names (1921 notebook), but they were not used in later years.

Middle Island: Small island in Karluk Lake between Gull and Camp Islands. Both Rich (1922 notebook) and Barnaby (1934 notebook) used this name.

Moraine Creek: Lateral creek on east shore at the north end of Karluk Lake 2.5 km southeast of the outlet. First named by Gilbert (1921 notebook).

Mount Shuman: Prominent mountain located 5 km southeast of Camp Island named in honor of FWS fishery biologist, Richard F. Shuman, who was killed in a plane crash in 1954. Shuman worked at Karluk Lake during 1943–49.

Murray Island (see also **Tern Island** and **Egg Islet**): Name first used by the ADFG in the 1970s for the small island in the middle of O'Malley Lake.

Nickoli's Barabara: Native shelter located at the Karluk River Portage.

North Fork of Upper Thumb River: North tributary branch of the Upper Thumb River that originates 5 km northeast of Thumb Lake. After joining the East Fork it forms the main Upper Thumb River that flows 0.8 km into the east end of Thumb Lake.

Northeast Harbor Creek: North-bank tributary to the lower Karluk River 2.5 km upstream from the lower weir site; first named by USBF weir foreman Ray S. Wood in 1928. Current U.S. Geological Survey topographic maps show that the lake origin of Northeast Harbor Creek flows into both Shelikof Strait and the Karluk River. This creek was also unofficially referred to as Katzinjammer Creek.

O'Malley Lake: Small lake (3.4 km long) tributary to the south end of Karluk Lake; first named by Gilbert and Rich in (1922 notebooks) for Henry O'Malley, U.S. Fish Commissioner. Gilbert originally called this **Upper Lake** (1921 notebook).

O'Malley River: Short terminal river outlet of O'Malley Lake that discharges into the south end of Karluk Lake. Gilbert originally called this **Lake Creek** (1921 notebook).

Ouzel Creek: Small creek on north shore of Thumb Lake. Barnaby first named Ouzel Creek in 1930 (notebook, 6 September 1930) and continued to use this name until 1934, but Bevan and Walker called it **Tuesday Creek** in the 1950s. Others called it **Thumb Lake Creek**. These names not currently used.

Oxbow: Curved side channel of the upper Karluk River 3 km downstream from Karluk Lake's outlet.

Pinguicula Lake: See **Barnaby Lake**.

Rich's Lagoon: Small spring-fed lateral creek entering somewhere near Little Lagoon Creek on east shore of Karluk Lake. First named by Barnaby in 1934 (notebook). During dry periods little surface water reached Karluk Lake from this source. Name not currently used.

River Ridge: See **Barnaby Ridge**.

Russell Creek: Small east-bank tributary of the Karluk River at the Portage. First named by Barnaby in 1930 (notebook) for USBF employee, J. R. "Bob" Russell, who each spring installed a temporary weir on the Karluk River to capture steelhead and take their eggs during 1927–32. Name not currently used.

Russellville: Fisheries research camp at the Karluk River Portage. Named for USBF employee Russell, who captured spring steelhead and took their eggs for hatchery incubation during 1927–32. Rich first recorded this name on a 1929 sketch map (notebook, 31 May 1929). The name continued to be used in the 1930s, but then gradually disappeared.

Salmon Creek: Lateral creek tributary to the south bank of Lower Thumb River just below the outlet of Thumb Lake.

Seven–Mile Beach: Long ocean beach located west of Uyak and running east–west for about 11 km (7 miles) along Shelikof Strait.

Shasta Creek: 1) Small (1.5 km) left–bank creek entering upper Karluk Lagoon. Karluk Lagoon hatchery (1896–1916) was located on this small creek (Moser 1902). 2) Small left-bank tributary of the Karluk River 8 km upstream from the lower weir site (USGS topographic map Karluk C-1).

Silver Salmon Creek: East-bank tributary of the Karluk River 5 km downstream of Karluk Lake's outlet.

Spring Creek: Small lateral spring-fed creek and small ponds at the north end of Karluk Lake 0.8 km east of the lake's outlet. First named by Gilbert (1921 notebook).

Stony Point: Land point on west shore of Karluk Lake 0.8 km northwest of Cascade Creek.

Sugarloaf Ditch: Ditch (2.5 km long) bringing water to the Karluk Lagoon hatchery (1896–1916) from the creek just to the east (Moser 1902). Clinton Gurnee called this stream Walom Creek on his 1903 map. Name not currently used.

Sugarloaf Peak: Mountain 1.5 km east of the Karluk Lagoon hatchery site (Moser, 1902). Name not currently used.

Tanglefoot Bay: Ocean bay on Shelikof Strait 2.5 km west of Karluk Spit. Site of Hume Canning and Trading Company's salmon cannery built in 1893.

Tent Point: Gravel land point on west shore of Karluk

Lake 2.5 km north of Grassy Point Creek. First named by Gilbert in 1921 (notebook).

Tent Point Creek: Small lateral creek on west shore of Karluk Lake just northwest of Tent Point. Gilbert and Rich first used this name in 1922 (notebooks).

Tern Island (also called **Murray Island** and **Egg Islet**)**:** Small island in center of O'Malley Lake. First named by Rich in his 1926 notebook.

The Slides: Steep rugged mountain escarpment that plunges into Shelikof Strait 1.5 km northeast of Karluk Spit.

Thumb Bay: Bay or basin of Karluk Lake east of Camp Island and Island Point; first named by Gilbert in 1921–22 (notebooks). This arm of Karluk Lake was often referred to as "the Thumb" by Rich (1926–1927 notebooks).

Thumb Island: See **Camp Island**.

Thumb Lake: Small lake (1.1 km long) tributary to the east shore of Karluk Lake.

Thumb Lake Creek: Small creek on northwest shore of Thumb Lake, possibly the same as **Ouzel Creek** or **Tuesday Creek**.

Thumb River: Terminal river discharging into the east shore of Karluk Lake 1.8 km southeast of Camp Island. The Thumb River has different names for each of its four river sections: 1) Lower Thumb River: the 0.8 km reach between Thumb and Karluk Lakes; 2) Upper Thumb River: the 0.8 km reach between Thumb Lake and the North and East Fork junction; 3) North Fork: the river fork flowing in from the north; and 4) East Fork: the river fork flowing in from the east. Gilbert and Rich called this **Thumb Creek** (1921–22 notebooks).

Tree Point: Land point on west shore of Karluk Lake 0.8 km south of Halfway Creek. Gilbert first called this **Cottonwood Point** for the cottonwood trees growing there (1921 notebook).

Tree Point Creek: Lateral creek on west shore of Karluk Lake 0.8 km south of Halfway Creek. First named by Rich in 1922 (notebook).

Tuesday Creek: See **Ouzel Creek**.

Upper Thumb River: This name has been used in two ways: 1) the 0.8 km river section between Thumb Lake and the North and East Fork junction, and 2) the entire river upstream of Thumb Lake, including the North Fork, East Fork, and main river between the forks junction and Thumb Lake. Gilbert and Rich called this **Upper Thumb Creek** (1922 notebooks).

Sockeye salmon fishermen at The Waterfalls, 4 km NE of Karluk Spit on Shelikof Strait, Kodiak Island, Alaska, ca. 1890. (From Porter, 1893)

Walom Creek: Small south-bank tributary to the Karluk River 0.8 km upstream of the east end of Karluk Lagoon. Walom Creek supplied water to Karluk Lagoon hatchery (1896–1916) through the 2.5 km Sugerloaf Ditch. Clinton Gurnee designated this stream as Walom Creek on his 1903 map. Name not currently used.

Waterfalls: Rugged coastal escarpment with two streams that cascade down its face into Shelikof Strait 3–5 km northeast of Karluk Spit. This was a prominent well-recognized landmark of fishermen working for the Karluk Spit salmon canneries in the early fishery.

Willow Creek: Name used for more than one Karluk Lake tributary. Gilbert used the name for **Cascade Creek** (1921 notebook), and Rich used it for **Alder Creek** (1926 notebook). Name not currently used.

Willow Point: Land point on east shore of Karluk Lake 2.5 km south of Island Point (shown on FRI map). Name not currently used.

APPENDIX 2

Glossary

Alevin (also called **sac fry**)**:** Early life stage of salmon between egg hatching and complete absorption of the yolk sac.

Alutiiq (plural: **Alutiit**)**:** The indigenous human population living in the cultural area that includes the Kodiak Archipelago, Prince William Sound, lower Kenai Peninsula, and southern Alaska Peninsula (Clark, 1984; Crowell et al., 2001). Over the years, many names have been used to identify Kodiak Island's indigenous people—Alutiiq, Koniag, Kadiaks, Pacific Eskimo, Qikertarmiut, Sugpiaq (plural, Sugpiat), and Aleut. The term "Alutiiq" has come into common usage since the early 1980s.

Artel: A Russian term for a small trading post or work crew during the 1700s–1800s in Alaska's history. A work group of hunters.

Baidarshchik: Chief of a Russian work crew who was also responsible for the management of the territory where his artel was located. Head of a hunting party.

Barabara: A Russian term for the wood and sod dwelling built by indigenous Alaskans on Kodiak Island and the Aleutians. These homes were partially excavated below ground and had a supporting wooden structure above ground that was covered with sod for protection from the elements. The Alutiiq people called these abodes "ciqluaq."

Beach seine (also called **haul seine** and **drag seine**)**:** The long nets that were used to encircle the sockeye salmon and haul them ashore at Karluk Spit in the early days of the commercial fishery.

Bug hunters: Humorous name given to the salmon research biologists (Gilbert, Rich, and Barnaby) during the 1920s–1930s by the Kodiak area management personnel and Karluk River weir tenders.

Case pack: Salmon cannery unit of production of 48 cans per case, each can weighing 1 pound (0.45 kg). The total weight of processed fish in one case is 21.8 kg. It took about 29–34 kg of live salmon to produce a case.

Chinook salmon (*Oncorhynchus tschawytscha*)**:** Also called **king, quinnat, spring,** and **tyee**; **tehavitche, tschavitche, tschawytscha, chavycha,** and **tchaviche** (Russian); and **amasuuk** (Alutiiq).

Chum salmon (*Oncorhynchus keta*)**:** Also called **dog** and **calico; hayko, hoikoh,** and **hyko** (Russian), and **alimaq** (Alutiiq).

Coho salmon (*Oncorhynchus kisutch*)**:** Also called **silver, silverside, skowitz, quisutsch,** and **hoopid salmon; medium red** (canning label); **kisutch** and **bielaya ryba** (Russian); and **qakiiyaq** (Alutiiq).

Dolly Varden (*Salvelinus malma*)**:** Also called **salmon trout** and **bull trout**; **goletz**, **golet**, and **malma** (in Siberia).

Fry: Early freshwater life stage of salmon immediately following the alevin stage. At emergence, sockeye salmon fry are about 27 mm long (range, 24–30 mm). In the Karluk fisheries literature, this term is sometimes used ambiguously. Most often it refers to the very early life stages after emergence from the redd site, migration to the nursery lake, and commencement of feeding, but at times it has been used for the entire freshwater residence. Nelson (1959) defined "fry" as "the period following the absorption of the yolk sac up to the time of active feeding," and "juvenile" as "the period commencing with feeding to the time of seaward migration." In actual practice at Karluk, the term "fry" often included the first few months of feeding, when the young sockeye salmon resided in the lake's littoral, before dispersing into the open limnetic zone.

Grilse (also called **Arctic salmon**)**:** Salmon that have one year or less of ocean growth before returning to their natal stream to spawn. These salmon are smaller than normal because of their brief period of ocean growth, but nevertheless they have mature gonads. Most grilse are males (known as "jacks"); rarely, grilse are small females (known as "jills"). At Karluk, 8 of the 24 recorded age combinations are grilse, though most of these rarely occur.

Juveniles: The early freshwater life stage of sockeye salmon between the start of active feeding and the time of smolt migration to the ocean. This life stage comprises essentially all of the young sockeye salmon's residence in the nursery lake (it varies from a few months to four years).

Kachemaz: Russian term for dried salmon similar to ukali, except that the salmon flesh is cut differently so the backbone is left in the carcass.

Kelts: Steelhead adults that survived their freshwater spawning act and returned downriver to the ocean.

Migrants (see also **Smolts**)**:** "Migrant" and "downstream migrant" were commonly used terms for sock-

eye salmon smolts at Karluk during 1920–40. Occasionally, the term "fingerlings" referred to smolts.

Odinochka: One man trading post, or a small administrative post, used to arrange barter with the Natives during the Russian period of Alaska's history. This can refer to a single log cabin manned by an overseer with 2–3 assistants.

Parr: Young salmon or trout residing in freshwater and showing dark bars or marks on their body sides.

Pavlovsk (also called **Kodiak** and **St. Paul**)**:** Russian village established in the late 1700s on northeastern Kodiak Island.

Pavlovsk Harbor: Saint Paul Harbor.

Pink salmon (*Oncorhynchus gorbuscha*)**:** Also called **humpback** and **humpy; gorbuscha** (Russian); **amartuq** (Alutiiq).

Promyshlenniks: Independent Russian traders and hunters; Russian fur hunters or trappers during Alaska's early history (late 1700s into 1800s).

Salt salmon: Early method of preserving salmon by storing them in a barrel with salt: 90.7 kg (200 pounds) of salt salmon per barrel. Salt salmon was prepared at Karluk by the Russians and Americans, especially in the 1800s and early 1900s. It required three barrels of salted salmon to produce one barrel of salted salmon bellies.

Sockeye salmon (*Oncorhynchus nerka*)**:** Also called **red salmon, redfish, blueback, saukeye, suckeye,** and **saw-qui; krasnoi riba, krasnaya ryba, krasnaya reba, krasnya ryba,** and **krasnaia ryba** (Russian); **niklliq, nee-klee-uk**, and **nuk kuk** (Alutiiq). The sockeye salmon's specific name, *nerka,* is a term that originated from the Koryak, the indigenous people of the Kamchatka Peninsula, Russia (Steller, 2003).

Smolts: Life stage of young salmon at the end of their freshwater residence when they change physiologically and migrate downstream to begin their ocean residence.

Traps (also called **pound nets**)**:** Fixed or floating netted devices that captured migrating adult salmon as they homed to their natal stream. Ocean traps were used prior to 1959 to capture Karluk's sockeye salmon along the west coast of Kodiak Island, but this fishing method became illegal when Alaska gained statehood.

Trout: Dolly Varden were called "trout" or "salmon trout" at Karluk in the late 1800s and early 1900s. Later, the term "trout" applied to rainbow or steelhead, and Dolly Varden were identified as charr.

Ukali (also called **yukala, ukala, iukola,** and **ukoli**)**:** A Russian term for salmon that were cleaned, split, and dried for food (it took about 10 kg of fresh salmon to make 1 kg of ukali). The drying process preserved the salmon and allowed it to be stored for months. Centuries before and after the Russian period in Alaska, dried fish (tammuq) was an important staple food in Alutiiq diets.

Zapor: A Russian term for the weir-like structure of wood and stones built across streams by Russians and Alutiit to impede the ascent of adult salmon and make them easier to harvest. Bean (1891) described "zapor" construction and Moser (1902) photographed Alaskan "zapors."

APPENDIX 3

Karluk Timeline

18,000 BC: Glaciers reached a maximum on Kodiak Island during the final Wisconsin phase of Pleistocene glaciation. On Kodiak Island this period was known as the Akalura glaciation, which followed at least two other periods of glaciation, the Sturgeon River (maximum 110,000 years ago) and Karluk (maximum 65,000 years ago) phases. During the Akalura glaciation, all of Kodiak Island was covered by glaciers, except for an ice-free area lying west of Karluk Lake. This ice-free area is known as the Kodiak Island Refugium since it provided habitat for the fauna and flora throughout the Akalura glaciation.

12,000–5000 BC: Climatic warming caused glaciers to retreat on Kodiak Island.

5500 BC: Probable first arrival of humans on Kodiak Island occurred.

4200 BC: Human habitation on Kodiak Island has been documented (first dated site) to this year.

3000 BC: Humans have continuously inhabited Karluk from at least 3000 BC to the present time. Prehistoric sites of human habitation in the Karluk vicinity include those at Karluk Village, numerous sites along the Karluk River, and at Karluk Lake. Many prehistoric sites contain evidence of occasional volcanic ash falls and tsunami waves.

1800 BC: Series of volcanic ash falls on Kodiak Island occurred.

20 BC: Ash fall at Karluk Lake occurred.

370 AD: Major ash fall at Karluk occurred.

1100–1850: Little Ice Age in the Northern Hemisphere caused glaciers in SW Alaska to advance somewhat during 1440–1710. On Kodiak Island, human population densities increased on the southwest end of the island and at Karluk. This climatic cooling caused humans to shift away from hunting sea mammals to greater reliance on salmon resources for subsistence.

1250: Tsunami wave at Karluk Village occurred.

1710: Ash fall at Karluk Lake occurred.

1741: Explorer Vitus Jonassen Bering (1681–1741), sailing from Russia, discovered Alaska and on his return voyage viewed Kodiak Island from a distance at sea. The German naturalist, Georg Wilhelm Steller (1709–1746), accompanied the Bering voyage of discovery to Alaska.

1761: Possible, but undocumented, landfall on Kodiak Island occurred by the Russian Dmitrii Pan'kov, skipper of the vessel *Sv. Vladimir.*

1762: First Russian map showing the presence of Kodiak Island produced.

1763–64: The Russian Stephen Glotov, skipper of the vessel *Sv. Andrean I Nataliia,* over-wintered at Russian Harbor on southwest Kodiak Island, but his presence was resisted by the Alutiiq inhabitants, forcing him to depart.

1763–75: Possible landfall on Kodiak Island occurred by an unknown Russian ship and crew, from which a map of southwest Kodiak Island was published in 1775.

1776: The Russian Dmitrii Polutov, skipper of the vessel *Sv. Arkangel Mikhail,* sailed along the south coast of Kodiak Island to Ugak Bay.

1779–80: The Russian Afanasii Ocheredin, skipper of the vessel *Sv. Kliment,* over-wintered on the southwest coast of Kodiak Island.

1784: The Russian merchant Grigorii I. Shelikhov established the first Russian colony at Three Saints Bay on the south coast of Kodiak Island.

1785–86: An exploration party of Russians, Aleuts, and Alutiiq dispatched by Shelikhov over-wintered at Karluk and established a small post. The Karluk River outlet to Shelikof Strait was then located at the northeast end of Karluk Spit. The Russians began harvesting and drying salmon from the Karluk River for their Native fur-hunting crews. They also prepared barrels of salted salmon for local use and, in later years, for export.

1786: First detailed Russian map showed the Kodiak Island coastline and location of the Karluk River and Cape Karluk.

1788: Large earthquake (magnitude 8) west of Kodiak Island caused coastal land subsidence and tsunami waves around Kodiak Island (July 1788).

1790: The Russian Aleksandr Andreyevich Baranov (1747–1819) became manager of Shelikhov's company in Alaska. He served in this position from 1790 to 1818, Shelikhov's venture becoming the Russian–American Company.

1792: Large earthquake hit Kodiak Island.

1792–93: Baranov moved the Russian colony at Three Saints Bay to Kodiak (then called Pavlovsk Gavan, or Paul's Harbor).

1794: The Russian Orthodox Church first came to Kodiak Island.

1795: Baranov conducted the first census of Kodiak Island, recording a population of 6206.

1804–05: Urey Lisiansky arrived on the Russian naval ship *Neva* and over-wintered at Kodiak. Based on this visit, he published a map of Kodiak Island in 1812 that showed the Karluk River and Lake.

1821: Russian–American Company obtained exclusive trading rights in Alaska.

1837–39: Smallpox epidemic decimated Alutiiq population on Kodiak Island.

before 1850: Karluk River entrance into Shelikof Strait shifted from the northeast to west end of Karluk Spit.

1866: First known photograph from Alaska was taken.

1867: United States purchased Alaska from Russia for $7,200,000. U.S. Army was given jurisdiction of Alaska in 1868.

1867: Three salt-salmon ventures began at the Karluk River, in addition to the salmon-drying operations.

1870: Alaska Fur Trading Company and Alaska Commercial Company began salt-salmon operations at the Karluk River.

1871: U.S. President Ulysses S. Grant signed bill creating the Commission of Fish and Fisheries (9 February).

1878: First salmon canneries in Alaska were established at Klawock and at old Sitka.

1880: Tarleton H. Bean, Ichthyologist, visited Kodiak (9–14 July) under the direction of the U.S. Commissioner of Fish and Fisheries to investigate the fish and fisheries of Alaska. Though he did not visit Karluk, he interviewed Charles Hirsch and others about the Karluk River fisheries. Sockeye salmon were then being harvested for salting and drying by Western Fur and Trading Company of San Francisco, CA, and by Oliver Smith and Charles Hirsch.

1882: First salmon cannery in central Alaska was operated on Karluk Spit by Oliver Smith and Charles Hirsch; their partnership became the Karluk Packing Company in 1884.

1888: Two additional salmon canneries were built and operated on Karluk Spit—Kodiak Packing Company and Aleutian Islands Fishing and Mining Company. A third cannery, Alaska Improvement Company, was built just to the west of the Karluk River mouth in 1888, but heavy seas wrecked their supply vessel, the bark *Julia Foard,* near the Karluk River mouth and delayed the start of their operations until 1889.

1888: Arctic Packing Company built a cannery near the mouth of Larsen Bay; the sockeye salmon for this cannery came from the Karluk River.

1888: Russian Orthodox Church was built at Karluk Village.

1888: U.S. Fish Commission was established as an independent agency and terminated its relationship with the Smithsonian Institution (20 January). Marshall McDonald was appointed U.S. Fish Commissioner.

1888–89: The large number of salmon canneries in Alaska caused over production of canned salmon, reducing market prices below production costs.

1889: Hume Packing Company built a cannery on Karluk Spit; Royal Packing Company and Russian–American Packing Company built canneries on Afognak Island and took sockeye salmon from the Karluk River.

1889: Dams, river barriers, or obstructions to salmon migrations were outlawed by the U.S. government (2 March 1889).

1889: Tarleton H. Bean visited the canneries and inspected fishery methods at Karluk Spit (2 August–7 September). He surveyed the spawning grounds at Karluk Lake (15–21 August) with Livingston Stone, Franklin Booth, and assistant Robert Lewis. Bean collected fish, birds, and plants at Karluk for the U.S. National Museum.

1889: Fishermen started beach seining in ocean waters outside Karluk Lagoon and river mouth. The 1882–1888 salmon harvests came from Karluk Lagoon and River.

1891: Karluk River Fisheries agreement between existing canneries apportioned the sockeye salmon pack. This agreement reduced the number of operating canneries and decreased packing expenses.

1891: Alaska Packers Association was formed in September to dispose of the salmon pack from Karluk.

1891: First salmon hatchery was operated by a private coalition of competing canneries (Karluk River Fisheries) for one year on Karluk Lagoon to enhance the sockeye salmon runs. They took 2,500,000 sockeye salmon eggs and released 500,000 fry into the brackish waters of Karluk Lagoon.

1892: Alaska Packing Association was formed to control production of canned salmon. This group included all canneries in the Kodiak area, except for the Alaska Improvement Company.

1892: Based on Livingston Stone's recommendation, Afognak Island was set aside as a Forest and Fish Cultural Reserve by the U.S. government (24 December 1892).

1893: Alaska Packers Association, with its headquarters in San Francisco, CA, incorporated to control the salmon pack (9 February). The number of operating canneries on Karluk Spit was reduced.

1893: Hume Canning and Trading Company built a salmon cannery at Tanglefoot Bay 2 km west of Karluk Spit; the cannery operated in 1893–94 and then was sold to the Alaska Packers Association in 1895.

1895: Alaska Packers Association's chartered ship *Raphael* wrecked in a severe storm near Tanglefoot Bay, losing the cargo of canned salmon.

1896: Steam power was first used to haul beach seines on Karluk Spit.

1896: Alaska Improvement Company used an experimental floating trap to capture salmon at Uganik Bay.

1896–1916: Second Karluk hatchery was operated by Alaska Packers Association on Karluk Lagoon to enhance sockeye salmon runs. From 1896 to 1916, they took 628,107,360 sockeye eggs and released 488,753,807 fry into the brackish waters of Karluk Lagoon. In 1903 the Karluk hatchery was enlarged.

1896–97: Fishery biologist, Cloudsley Louis Rutter, worked as a fish culturist at the new Karluk hatchery. He visited the upper Karluk River and Lake, and collected fishes, birds, and plants.

1897: U.S. Fish Commission biologist, Alvin B. Alexander, briefly studied Karluk's salmon fishery (18 July–6 August); Captain Jefferson F. Moser, Commander, U.S. Fish Commission steamer *Albatross,* made two stops at Karluk, one in July, another in August.

1897: Pacific Steam Whaling Company and Hume Brothers and Hume built salmon canneries at Uyak Anchorage and harvested sockeye salmon from Karluk.

1897: For the first time, salmon harvests at Karluk were recorded separately by species.

1898: Karluk River and Lagoon were closed to commercial salmon fishing, except for hatchery procurement of brood stock and for subsistence use by Karluk's residents (7 May).

1900: U.S. Treasury Department mandated that canneries build sockeye salmon hatcheries and release four fry for every adult caught (2 May).

1900: Alaska Packers Association's bark *Merom* wrecked on the rocks near Karluk Spit with 12,572 cases of canned salmon.

1901: Alaska Packers Association purchased the first of its *Star* fleet, which soon grew to nearly 20 iron and steel, square-rigged, sailing ships. The ships were used to haul workers and equipment north to the salmon fishing grounds and canneries and to return workers and a cargo of canned salmon south to San Francisco, CA.

1902: U.S. Treasury Department increased its hatchery mandate to 10 fry released for every sockeye salmon adult caught (24 January).

1903: U.S. Bureau of Fisheries was created in the Department of Commerce and Labor (1 July). Supervision of Alaska's salmon and fur seals transferred from Treasury Department to U.S. Bureau of Fisheries.

1903: U.S. President Theodore Roosevelt ordered the formation of the Alaska Salmon Commission to determine the conditions of Alaska's salmon fisheries. Field studies were conducted in 1903 using the U.S. Fish Commission steamer *Albatross,* with David Starr Jordan, Barton Warren Evermann, Franklin Swift, Alvin B. Alexander, J. Nelson Wisner, and Cloudsley L. Rutter. Special assistants were Frederic M. Chamberlain, E. L. Goldsborough, Harold Heath, Charles H. Gilbert, Milo H. Spaulding, Harold Bowen Jordan, Harry C. Fassett, and A. H. Baldwin.

1903: U.S. Fish Commission fishery biologist, Cloudsley Louis Rutter, studied sockeye salmon at Karluk River and Lake (May–August), assisted by Milo H. Spaulding. Rutter died in November 1903, shortly after completing his field work at Karluk; his 1903 studies were later published by Frederic M. Chamberlain (1907).

1903: Alaska Packers Association doubled the original size of the Karluk hatchery.

1906: U.S. Secretary of Commerce and Labor approved the Karluk hatchery (29 June). James A. Richardson, Fish Culturist and builder of the Karluk hatchery (1896), was replaced as Superintendent by Ingwald Loe. Federal government began to grant rebates of case pack taxes to canneries that operated hatcheries (40 cent rebate for every 1,000 sockeye salmon fry released from the hatchery).

1907: Alaska Packers Association's bark *Servia* was driven ashore in a gale at Karluk with a full cargo of canned salmon.

1907–08: U.S. Bureau of Fisheries salmon hatchery was constructed on Afognak Lake (Litnik Lake) near the site originally selected by Livingston Stone in 1889.

1909: Alaska Packers Association began to build a new salmon cannery at Larsen Bay to replace its facilities at Karluk Spit.

1909–12: Charles H. Gilbert of Stanford University used scales to age salmon from the Columbia and Fraser Rivers.

1911: Alaska Packers Association ceased cannery operations at Karluk Spit, but continued to harvest sockeye salmon at Karluk for its new Larsen Bay cannery. Besides the traditional beach seining at Karluk Spit, there was greater use of purse seines and gill nets to

capture sockeye salmon. Only subsistence harvests were allowed in Karluk Lagoon.

1911: U.S. Bureau of Fisheries made a brief reconnaissance of the Karluk River and Lake.

1912: Novarupta volcano erupted at Katmai on the Alaska Peninsula opposite Kodiak Island, spreading ash over the island, but only small accumulations occured in the Karluk area.

1912: Alaska was given formal territorial status.

1913: U.S. Department of Commerce and Labor was divided into two departments; the Bureau of Fisheries was placed in the Department of Commerce (4 March).

1916: U.S. Bureau of Fisheries employee, Edward M. Ball, briefly investigated the sockeye salmon spawning grounds of the Karluk River and Lake.

1916: Alaska Packers Association permanently closed the Karluk hatchery, the remaining eggs being transferred to Afognak Hatchery (30 June).

1916: Alaska Packers Association merged with California Packing Corporation, which adopted the name Del Monte Corporation in the 1960s.

1918: Karluk River and Lagoon was closed to commercial salmon fishing, except for Native subsistence. Commercial fishing was allowed in the ocean 91 m beyond the Karluk River mouth.

1919: Charles H. Gilbert and U.S. Bureau of Fisheries employee Henry O'Malley briefly visited Karluk Lake to view the spawning habitats of sockeye salmon.

1919: Edward M. Ball recommended that the Karluk River watershed be placed in a National Fisheries Reservation.

1921: The first salmon counting weir in Alaska was installed on the Karluk River under the general direction of Charles H. Gilbert and Henry O'Malley. The weir was located on the lower Karluk River at the eastern end of Karluk Lagoon. Gilbert and O'Malley inspected the weir operations and visited Karluk Lake.

1922: Willis H. Rich became Chief of the U.S. Bureau of Fisheries, Division of Scientific Inquiry. Henry O'Malley became U.S. Commissioner of Fisheries.

1922–33: The only legal commercial salmon fishing gear during this time were beach seines, gill nets, and stationary traps.

1924: The U.S. Government passed the White Act that required 50% escapement of the total sockeye salmon run. Purse seines and floating traps for catching salmon were prohibited in the Kodiak area. First stationary traps were used to capture sockeye salmon during their ocean migration along the northwest coast of Kodiak Island (Rich and Ball, 1931), although a few traps may have operated in Uganik Bay in 1919–22 (Roppel, 1986).

1926–31: Chauncey Juday, Willis H. Rich, George I. Kemmerer, and Albert Mann conducted limnological studies of Karluk Lake; they published their results in 1932.

1927: Gilbert and Rich published the results of their sockeye salmon studies at Karluk.

1927: At the request of Willis Rich, a small cabin was built on Camp Island, Karluk Lake, for use by U.S. Bureau of Fisheries research biologists.

1927–32: Steelhead eggs were taken annually from the Karluk River at the Portage by the U.S. Bureau of Fisheries for incubation at Afognak hatchery and at Seward. A temporary weir was installed each spring across the Karluk River to capture mature steelhead moving downstream and to take the eggs, which were incubated for a few weeks onsite in a small tributary of the Karluk River.

1929: Stock market crashed and the Great Depression started.

1929: This was the final year that any of the *Star* fleet of the Alaska Packers Association carried workers and supplies north and returned south with a cargo of canned salmon.

1929: U.S. Bureau of Fisheries used 24 vessels and one airplane to regulate the Pacific salmon fisheries.

1930: Karluk research biologist, Willis Rich, resigned as U.S. Bureau of Fisheries Director of Pacific Fisheries Investigations, to become Professor of Zoology at Stanford University.

1930–37: Joseph Thomas Barnaby of Stanford University and U.S. Bureau of Fisheries conducted studies at Karluk Lake and River, including smolt-to-adult survival of sockeye salmon, water chemistry of Karluk Lake, and Dolly Varden migration and food habits.

1931: U.S. Bureau of Fisheries, Fisheries Biological Laboratory (Montlake Laboratory) opened in Seattle, WA (22 May). U.S. Bureau of Fisheries personnel at the Stanford University field station transferred to the Montlake Laboratory.

1933: Depth of the Great Depression. These economic hard times continued through the 1930s. Tight budgets at U.S. Bureau of Fisheries affected management and research of Karluk's sockeye salmon.

1933: Purse seines were ruled legal for commercial salmon fishing in Alaska.

1933: Afognak hatchery was permanently closed by U.S. Commissioner of Fisheries, Frank T. Bell (30 June).

1935–37: U.S. Bureau of Fisheries biologist Joseph Thomas Barnaby studied Dolly Varden migration and food habits at Karluk; these charr studies continued until 1941 by biologists Allan C. DeLacy and William M. Morton.

1939: U.S. Bureau of Fisheries was transferred from Department of Commerce to Department of the Interior (1 July).

1939–1945: World War II. U.S. military controlled the airspace and waters around Kodiak Island.

1940: U.S. Bureau of Fisheries and Bureau of Biological Survey consolidated as the Fish and Wildlife Service in the Department of the Interior (30 June).

1940: Suspension bridge was built across Karluk River between Karluk Village and Karluk Spit.

1941: Dolly Varden bounty was discontinued in Alaska.

1941: Kodiak National Wildlife Refuge was established by President Franklin D. Roosevelt to protect the habitat of the Kodiak brown bear (Executive Order 8857, dated 19 August 1941). Karluk Lake and River were included within the refuge boundaries.

1942: Attu and Kiska Islands in the Aleutians were captured by Japanese armed forces (6–7 June); U.S. military began buildup on Kodiak Island.

1942: Salmon counting weir was moved from lower Karluk River to the Portage, where it operated for three years (1942–44).

1943: Secretary of the Interior Ickes created the Karluk Reservation for the Alutiiq people (Public Land Order 128). The reservation included about 35,000 acres of land and water near Karluk Spit, including prime ocean beach seining locations.

1944: U.S. Fish and Wildlife Service biologist, Joseph Thomas Barnaby, published his research on Karluk's sockeye salmon.

1945: Salmon counting weir was moved from the Portage to near the outlet of Karluk Lake, where it operated for the next 30 years.

1946: Purse seines were prohibited within 457 m of the Karluk River mouth.

1947: The Fisheries Research Institute, University of Washington, Seattle, was formed; first Director was William F. Thompson.

1947: U.S. Fish and Wildlife Service biologist, Richard F. Shuman, studied bear predation on sockeye salmon adults at Karluk Lake.

1948–49: Fisheries Research Institute biologist, Donald E. Bevan, studied ocean migration of sockeye salmon along the west coast of Kodiak Island and found that many home to the Karluk River.

1948–55: Fisheries Research Institute biologists studied Karluk's sockeye salmon. Topics included ocean migrations, ages, sizes, and spawning habitats of the adults, and sizes and ages of the juveniles.

1949: U.S. Supreme Court ruled on *Hynes v. Grimes Packing Co. et al (*337 U.S. 86) that 1) the Secretary of the Interior Ickes had the authority to establish the Karluk Reservation in 1943, and 2) Karluk residents could not bar the access of others to the waters and fish within the reservation.

1949: U.S. Fish and Wildlife Service biologists, Richard Shuman and Philip R. Nelson, searched for a suitable lake on Kodiak Island to study the effects of artificial fertilization on lake productivity. Bare Lake, located 25 km SW of Karluk Lake, was selected for the fertilization experiment.

1949: Alaska Department of Fisheries was created by the Alaska Territorial Legislature; Clarence L. Anderson became its first Director.

1950: William F. Thompson, Director of the Fisheries Research Institute, proposed that the productive midseason runs of Karluk's sockeye salmon have been depleted by commercial fishing.

1950–56: U.S. Fish and Wildlife Service fishery biologist, Philip Nelson, fertilized Bare Lake with inorganic phosphate and nitrates and studied the response in the plankton and young sockeye.

1953: Bounty was repealed on bald eagles in Alaska. The first eagle bounty was implemented in 1917; 114,291 bald eagles were killed in 1917–40. An eagle bounty existed during some, but not all, years in the 1940s.

1953–59: Steelhead eggs were taken at the Karluk River Portage by the Kodiak Conservation Club, Alaska Department of Fish and Game, and U.S. Fish and Wildlife Service, in cooperation with the U.S. Navy. A temporary V-shaped weir was installed each spring to capture mature steelhead moving downstream and the eggs were flown to Devils Creek Hatchery on the Kodiak Naval Base.

1955: U.S. Fish and Wildlife Service was split into Bureau of Commercial Fisheries and Bureau of Sport Fisheries and Wildlife (1 July).

1956: All federal biological research on Alaska's finfish moved from Montlake Biological Laboratory, Seattle, WA, to Juneau, AK.

1957: Alaska Department of Fish and Game was created by the Alaska Territorial Legislature, with Clarence L. Anderson as the first Director (1 April). ADFG replaced the Alaska Department of Fisheries.

1958: U.S. Fish and Wildlife Service biologist, George A. Rounsefell, published a paper on the reasons for the decline in Karluk's sockeye salmon runs.

1958: Fish traps were prohibited in the Kodiak Island region for commercial salmon fishing.

1959: Alaska officially became 49th state of the United States (3 January).

1960: State of Alaska assumed responsibility for managing its fisheries from the U.S. Government (1 January).

1960: U.S. Bureau of Commercial Fisheries built a field research laboratory and living facilities on Camp Island, Karluk Lake.

1960: U.S. Fish and Wildlife Service, Auke Bay Biological Laboratory, opened near Juneau, AK.

1960–70: U.S. Bureau of Commercial Fisheries conducted research on Karluk's sockeye salmon, including its genetics, migratory behavior and timing, abundance of smolt outmigration, fecundity, bear predation, and subpopulations.

1962: U.S. Bureau of Commercial Fisheries biologists John B. Owen, Charles Y. Conkle, and Robert F. Raleigh reviewed past research and published a report on sockeye salmon production at Karluk.

1964: Large earthquake hit southern Alaska (magnitude 9.2) and created a tsunami that damaged Kodiak; little damage occurred at Karluk Village (March 27). Karluk Lagoon subsided about 46 cm.

1967: Alaska Department of Fish and Game assumed fully responsibility for operating the Karluk River weir. Alaska Department of Fish and Game began rehabilitation research on Karluk's sockeye salmon.

1969: U.S. Bureau of Commercial Fisheries ended its long-term sockeye salmon research program at Karluk Lake.

1969: Alaska Department of Fish and Game investigated ways to rehabilitate Karluk's sockeye runs.

1970: U.S. Bureau of Commercial Fisheries was renamed the National Marine Fisheries Service (3 October) and became part of the National Oceanic and Atmospheric Administration within the Department of Commerce.

1971: Alaska Department of Fish and Game, Division of Fisheries Rehabilitation, Enhancement and Development (FRED) was created by the Alaska State Legislature.

1971: Alaska Native Land Claims Settlement Act allowed Native corporations to select lands for ownership.

1972: Commercial Fisheries Limited Entry Commission was created by the Alaska State Legislature.

1972: Alaska Packers Association closed its salmon cannery at Larsen Bay.

1973: Limited entry permit system went into effect for commercial salmon fishing in Alaska.

1973: University of Washington biologists Richard Van Cleve and Donald E. Bevan published a paper on the reasons for the decline in Karluk's sockeye salmon runs.

1976: Salmon counting weir was moved from Karluk Lake's outlet to the lower river; the weir has continued to operate at this site to the present time (2010).

1976: Alaska State Legislature directed the Commissioner of the Department of Fish and Game to develop comprehensive regional salmon plans.

1978: The Karluk Native Corporation (later merged with the Koniag Corporation) assumed ownership of the entire Karluk River and northern half of Karluk Lake and pursued several income producing ventures in the Karluk basin, including 1) bear watching platforms, 2) sport fishing for steelhead, king salmon, sockeye salmon, coho salmon, and Dolly Varden, and 3) Karluk River float trips.

1978: A violent storm with strong NE winds (>160 km per hour) breached Karluk Spit and changed the course of the lower Karluk River (January). The suspension bridge between Karluk Spit and New Karluk Village was destroyed, as were many of the remaining cannery buildings. Karluk residents moved the village 1.5 km inland, aided by the U.S. Army Corps of Engineers. The new location included 23 new homes, a land based airstrip (820 m), and a new school (1982).

1978: The National Marine Fisheries Service transferred their research field station on Camp Island, Karluk Lake, to the U.S. Fish and Wildlife Service, Kodiak National Wildlife Refuge.

1978–86: Alaska Department of Fish and Game rehabilitated the Upper Thumb River sockeye run by culturing eggs to the eyed stage and implanting them into the river. Eggs were first incubated at Devil's Creek Hatchery in Kodiak and then at Kitoi Hatchery, Afognak Island (1978–79). A streamside hatchery was operated on the East Fork of Upper Thumb River in 1980–86. During 1978–86, they took 101,217,000 sockeye eggs and planted 82,546,000 upstream of natural fish barriers in the Upper Thumb River drainage. This rehabilitation project was led by Fishery Biologist Lorne E. White, Division of Fisheries Rehabilitation, Enhancement, and Development.

1979: Alaska Department of Fish and Game launched the statewide limnology program in the Division of Fisheries Rehabilitation, Enhancement and Development (FRED) to enhance sockeye salmon nursery lakes through nutrient enrichment and fry stocking. Regular limnological sampling of many physical,

chemical, and biological factors has occurred at Karluk Lake from 1979 to the present time.

1980: The Karluk Native Corporation merged with the regional corporation, Koniag, Inc. (December).

1982: U.S. Fish and Wildlife Service established the position of Fishery Biologist for the Kodiak National Wildlife Refuge.

1982–88: U.S. Fish and Wildlife Service (Anchorage and Seattle offices) studied Karluk Lake, including stickleback competition with young sockeye, predation on juvenile sockeye by charr and young coho salmon, and past lake fertility revealed by lake sediments. Other projects included measurement of smolt outmigration and movements of adult steelhead and coho salmon in the Karluk River.

1983: Kodiak Regional Aquaculture Association (KRAA) was approved by the Alaska Department of Fish and Game (17 June).

1984: Kodiak Regional Comprehensive Salmon Plan Phase I, 1982–2002, was approved by the Alaska Department of Fish and Game (April 13). Phase II was approved in 1987 (15 September) and a revision to Phase II was approved in 1992 (27 April).

1986–90: Alaska Department of Fish and Game added artificial fertilizers to the north basin of Karluk Lake to enhance its productivity. The amount of fertilizer added was 87,272 kg (1986), 87,272 kg (1987), 87,272 kg (1988), 77,272 kg (1989), and 86,363 (1990).

1986–91: University of Alaska biologist Thomas C. Kline, Jr. measured the proportion of marine-derived nitrogen present in the juveniles and adults of Karluk's sockeye salmon.

1987: Alaska Department of Fish and Game limnologists Jeffery P. Koenings and Robert D. Burkett published their Aquatic Rubic's Cube paper concerning Karluk's sockeye salmon and the importance of the lake rearing environment. They recommended artificial fertilization of Karluk Lake.

1989: *Exxon Valdez* oil spill (24 March) halted all commercial salmon fishing on Kodiak Island for the entire year.

1997–98: Alaska Department of Fish and Game biologist Dana Schmidt and colleagues published papers on Karluk's sockeye salmon that show the importance of salmon-carcass nutrients to Karluk Lake's fertility and salmon production.

1994–2004: University of Alaska biologist Bruce Finney and his graduate students and colleagues studied marine-derived nitrogen and plankton microfossils in Karluk Lake's sediments and related those to the past 2200 years of sockeye escapements. Salmon-carcass nutrients affect the lake's trophic status. Ocean climate affects the long-term variations in escapements and lake fertility.

2008–09: U.S. National Marine Fisheries Service biologists Ellen C. Martinson and John H. Helle and their colleagues studied the scales of age 2.2 early-run Karluk sockeye salmon to determine salmon growth and survival in relation to climatic and oceanic regimes.

APPENDIX 4

Kodiak Area Management Reports, 1924–2010

1924: Fred R. Lucas. Report of Kodiak-Afognak Fisheries District to August 31, 1924. U.S. Bureau of Fisheries, Afognak, AK (5 September 1924). 8 p.

1924: Fred R. Lucas. Report of Kodiak-Afognak District for the month of September 1924, including the inspection of the Karluk and Uganik spawning areas. U.S. Bureau of Fisheries, Afognak, AK (4 October 1924). 9 p.

1928: Howard H. Hungerford. Report of operations, Kodiak-Afognak District, 1928. U.S. Bureau of Fisheries.

1929: Howard H. Hungerford. Report of operations, Kodiak-Afognak District, 1929. U.S. Bureau of Fisheries.

1930: Howard H. Hungerford. Report of operations, Kodiak-Afognak District, 1930. U.S. Bureau of Fisheries.

1931: Howard H. Hungerford. Report of operations, Kodiak-Afognak District, 1931. U.S. Bureau of Fisheries.

1932: Howard H. Hungerford. Report of operations, Kodiak-Afognak District, 1932. U.S. Bureau of Fisheries.

1933: Howard H. Hungerford. Report of operations, Kodiak-Afognak District, 1933. U.S. Bureau of Fisheries, Seattle, WA (27 January 1934).

1934: Charles P. Turner. Report of operations, Kodiak-Afognak District, 1934. U.S. Bureau of Fisheries. 49 p.

1935: Charles P. Turner. Report of operations, Kodiak-Afognak District, 1935. U.S. Bureau of Fisheries.

1936: Charles P. Turner. Report of operations, Kodiak-Afognak District, 1936. U.S. Bureau of Fisheries.

1937: J. Steele Culbertson. Kodiak-Afognak District, 1937, Report of fishery operations. U.S. Bureau of Fisheries. 22 p.

1938: J. Steele Culbertson. Kodiak-Afognak District, 1938, Report of fishery operations. U.S. Bureau of Fisheries. 44 p.

1939: Ralph A. Ferrandini. Kodiak-Afognak District, 1939, Report of fishery operations. U.S. Bureau of Fisheries. 40 p.

1940: Ralph A. Ferrandini. Kodiak-Afognak Report, 1940, Alaska fishery operations. U.S. Fish and Wildlife Service. 45 p.

1941: Ralph A. Ferrandini. Kodiak-Afognak Report, 1941, Alaska fishery operations. U.S. Fish and Wildlife Service. 41 p.

1942: Charles Petry. Annual report of operations in the Kodiak District, 1942. U.S. Department of the Interior, Fish and Wildlife Service. 56 p.

1943: Mark A. Logan. Annual report, Kodiak-Afognak, 1943. U.S. Fish and Wildlife Service, Seattle, WA (17 January 1944). 37 p.

1944: Marcus W. Meyer. Annual report, Kodiak District, 1944. U.S. Fish and Wildlife Service. 52 p.

1945: Marcus W. Meyer. Annual report, Kodiak District, 1945. U.S. Fish and Wildlife Service. 90 p.

1946: Marcus W. Meyer. Annual report, Kodiak District, 1946. U.S. Fish and Wildlife Service. 64 p.

1947: Marcus W. Meyer. Annual report, Kodiak District, 1947. U.S. Fish and Wildlife Service. 55 p.

1948: Marcus W. Meyer. Annual report, Kodiak District, 1948. U.S. Department of the Interior, Fish and Wildlife Service, Alaska Fisheries Division. 45 p.

1949: Roy R. Lindsley. Annual report, Kodiak District, 1949. U.S. Department of the Interior, Fish and Wildlife Service, Branch of Alaska Fisheries. 27 p.

1950: Roy R. Lindsley. Annual report, Kodiak District, 1950. U.S. Department of the Interior, Fish and Wildlife Service, Branch of Alaska Fisheries. 28 p.

1951: Roy R. Lindsley. Annual report, Kodiak District, 1951. U.S. Department of the Interior, Fish and Wildlife Service, Branch of Alaska Fisheries. 30 p.

1952: Roy R. Lindsley. Annual report, Kodiak area, 1952. U.S. Department of the Interior, Fish and Wildlife Service, Branch of Alaska Fisheries. 27 p.

1953: Roy R. Lindsley. Annual report, Kodiak area, 1953. U.S. Department of the Interior, Fish and Wildlife Service, Branch of Alaska Fisheries. 24 p.

1954: U.S. Fish and Wildlife Service. Annual report, Kodiak area, 1954. U.S. Department of the Interior, Fish and Wildlife Service, Branch of Alaska Fisheries. 24 p.

1955: U.S. Fish and Wildlife Service. Annual report, Kodiak area, 1955. U.S. Department of the Interior, Fish and Wildlife Service, Branch of Alaska Fisheries. 24 p.

1956: U.S. Fish and Wildlife Service. Annual report, Kodiak area, 1956. U.S. Department of the Interior, Fish and Wildlife Service, Alaska Commercial Fisheries. 20 p.

1957: U.S. Fish and Wildlife Service. Annual report, Kodiak area, 1957. U.S. Department of the Interior, Fish and Wildlife Service, Alaska Commercial Fisheries. 20 p.

1958: Charles F. Connelley, Jr. Annual report, Kodiak area, 1958. U.S. Department of the Interior, Fish and

Wildlife Service, Alaska Commercial Fisheries. 29 p.

1959: Charles F. Connelley, Jr. Annual report, Kodiak area, 1959. U.S. Department of the Interior, Fish and Wildlife Service, Alaska Commercial Fisheries. 37 p.

1960: Robert J. Simon and Robert S. Roys. Kodiak area annual report, 1960. Alaska Department of Fish and Game, Commercial Fisheries Division, Kodiak. 31 p.

1961: Dexter F. Lall and Robert S. Roys. Kodiak area annual report, 1961. Alaska Department of Fish and Game, Commercial Fisheries Division, Kodiak. 46 p.

1962: Robert J. Simon, Dexter F. Lall, and Robert S. Roys. Kodiak area annual report, 1962. Alaska Department of Fish and Game, Commercial Fisheries Division, Kodiak. 51 p.

1963: Robert J. Simon, Dexter F. Lall, and Larry B. Jennings. Kodiak area annual report, 1963. Alaska Department of Fish and Game, Commercial Fisheries Division, Kodiak. 43 p.

1964: Robert J. Simon, Dexter F. Lall, and Larry B. Jennings. Kodiak area annual report, 1964. Alaska Department of Fish and Game, Commercial Fisheries Division, Kodiak.

1965: Robert J. Simon, Dexter F. Lall, and Larry B. Jennings. Kodiak area annual report, 1965. Alaska Department of Fish and Game, Commercial Fisheries Division, Kodiak.

1966: Robert J. Simon, Dexter F. Lall, Paul C. Pedersen, and Melvan C. Morris, Jr.. Kodiak area annual report, 1966. Alaska Department of Fish and Game, Division of Commercial Fisheries.

1967: Kodiak Area Management Staff. Kodiak area annual report, 1967. Alaska Department of Fish and Game, Division of Commercial Fisheries.

1968: Robert J. Simon, Jack Lechner, Peter Jackson, and Martin Eaton. Kodiak area management annual report, 1968. Alaska Department of Fish and Game.

1969: Robert J. Simon, Jack Lechner, Martin F. Eaton, and Peter B. Jackson. Kodiak area management annual report, 1969. Alaska Department of Fish and Game.

1970: Robert J. Simon, Jack Lechner, Martin F. Eaton, Peter B. Jackson, and Louis A. Gwartney. Kodiak area management annual report, 1970. Alaska Department of Fish and Game. 128 p.

1971: Robert J. Simon, Jack Lechner, Martin F. Eaton, and Louis A. Gwartney. Kodiak area management annual report, 1971. Alaska Department of Fish and Game.

1972: Jack Lechner, Martin F. Eaton, Kenneth R. Manthey, Louis A. Gwartney, and Lawrence M. Malloy. Kodiak area management annual report, 1972. Alaska Department of Fish and Game.

1973: Jack Lechner, Paul C. Pedersen, Kenneth R. Manthey, Louis A. Gwartney, and Lawrence M. Malloy. Kodiak area management annual report, 1973. Alaska Department of Fish and Game.

1974: Ken Manthey, Larry Malloy, and Joan Peterson. Annual management report, 1974, Kodiak Management Area. Alaska Department of Fish and Game, Division of Commercial Fisheries, Kodiak. 134 p.

1975: Ken Manthey, Larry Malloy, and Melayna McGuire. 1975 annual management report, Kodiak Management Area. Alaska Department of Fish and Game, Division of Commercial Fisheries, Kodiak. 160 p.

1976: Ken Manthey, Larry Malloy, and Yolanda Servin. 1976 annual management report, Kodiak Management Area. Alaska Department of Fish and Game, Division of Commercial Fisheries, Kodiak. 174 p.

1977: Ken Manthey, Larry Malloy, and Linda Wright. 1977 annual management report, Kodiak Management Area. Alaska Department of Fish and Game, Division of Commercial Fisheries, Kodiak. 179 p.

1978: Ken Manthey, Larry Malloy, and Linda Wright. 1978 annual management report, Kodiak Management Area. Alaska Department of Fish and Game, Division of Commercial Fisheries, Kodiak. 231 p.

1979: Ken Manthey, Larry Malloy, and Linda Wright. 1979 annual management report, Kodiak Management Area. Alaska Department of Fish and Game, Division of Commercial Fisheries, Kodiak. 256 p.

1980: Ken Manthey, Larry Malloy, and Linda Wright. 1980 annual management report, Kodiak Management Area. Alaska Department of Fish and Game, Division of Commercial Fisheries, Kodiak. 246 p.

1981: Ken Manthey, Dave Prokopowich, and Linda Wright. 1981 annual management report, Kodiak Management Area. Alaska Department of Fish and Game, Division of Commercial Fisheries, Kodiak. 255 p.

1982: Ken Manthey, Dave Prokopowich, and Linda Wright. 1982 annual management report, Kodiak Management Area. Alaska Department of Fish and Game, Division of Commercial Fisheries, Kodiak. 315 p.

1983: Ken Manthey, Dave Prokopowich, and Linda

Wright. 1983 annual finfish management report, Kodiak Management Area. Alaska Department of Fish and Game, Division of Commercial Fisheries, Kodiak. 354 p.

1984: Ken Manthey, Dave Prokopowich, and JoAnn Strickert. 1984 annual finfish management report, Kodiak Management Area. Alaska Department of Fish and Game, Division of Commercial Fisheries, Kodiak. 338 p.

1985: Ken Manthey, Dave Prokopowich, and JoAnn Strickert. 1985 annual finfish management report, Kodiak Management Area. Alaska Department of Fish and Game, Division of Commercial Fisheries, Kodiak. 415 p.

1986: Alaska Department of Fish and Game. 1995. Kodiak Management Area annual salmon management report, 1986 and 1987. Alaska Department of Fish and Game, Division of Commercial Fisheries, Kodiak, Regional Information Report No. 4K95-5.

1987: Alaska Department of Fish and Game. 1995. Kodiak Management Area annual salmon management report, 1986 and 1987. Alaska Department of Fish and Game, Division of Commercial Fisheries, Kodiak, Regional Information Report No. 4K95-5.

1988: Lawrence M. Malloy and David L. Prokopowich. 1992. Kodiak Management Area annual finfish management report, 1988. Alaska Department of Fish and Game, Division of Commercial Fisheries, Kodiak, Regional Information Report 4K92-7 (February, 1992). 269 p.

1989: Kevin Brennan, Larry Malloy, Dave Prokopowich, and Dennis Gretsch. 1992. Kodiak Management Area, annual salmon management report, 1989. Alaska Department of Fish and Game, Division of Commercial Fisheries, Kodiak, Regional Information Report No. 4K92-30 (August, 1992). 262 p.

1990: Joan R. Brodie, Kevin R. Brennan, and Larry Malloy. 1997. Kodiak Management Area annual commercial and subsistence salmon management report, 1990. Alaska Department of Fish and Game, Commercial Fisheries Management and Development Division, Kodiak, Regional Information Report No. 4K97-5.

1991: Dennis Gretsch, Kevin Brennan, and Dave Prokopowich. 1992. Kodiak Management Area, annual finfish management report, 1991. Alaska Department of Fish and Game, Division of Commercial Fisheries, Kodiak, Regional Information Report 4K92-37 (October, 1992). 170 p.

1992: Kevin Brennan, David Prokopowich, and Dennis Gretsch. 1993. Kodiak Management Area, commercial salmon annual management report, 1992. Alaska Department of Fish and Game, Division of Commercial Fisheries, Kodiak, Regional Information Report No. 4K93-28 (October, 1993). 278 p.

1993: Kevin Brennan. 1995. Kodiak Management Area commercial salmon annual management report, 1993. Alaska Department of Fish and Game, Commercial Fisheries Management and Development Division, Kodiak, Regional Information Report No. 4K95-3.

1994: Kevin Brennan, Dave Prokopowich, and Dennis Gretsch. 1996. Kodiak Management Area, commercial salmon annual management report, 1994. Alaska Department of Fish and Game, Commercial Fisheries Management and Development Division, Kodiak, AK, Regional Information Report No. 4K96-38 (July, 1996). 277 p.

1995: Kevin Brennan, Dave Prokopowich, and Dennis Gretsch. 1997. Kodiak Management Area commercial salmon annual management report, 1995. Alaska Department of Fish and Game, Commercial Fisheries Management and Development Division, Kodiak, Regional Information Report No. 4K97-30.

1996: Kevin Brennan. 1998. Kodiak Management Area commercial salmon annual management report, 1996. Alaska Department of Fish and Game, Commercial Fisheries Management and Development Division, Kodiak, AK, Regional Information Report No. 4K98-35 (June, 1998).

1997: Kevin Brennan. 2000. Kodiak Management Area commercial salmon annual management report, 1997. Alaska Department of Fish and Game, Division of Commercial Fisheries, Kodiak, Regional Information Report 4K00-27.

1998: Dave L. Prokopowich. 2000. Kodiak Management Area commercial salmon annual management report, 1998. Alaska Department of Fish and Game, Division of Commercial Fisheries, Kodiak, Regional Information Report No. 4K00-2.

1999: Jeff A. Wadle and Kevin Brennan. 2001. Kodiak Management Area commercial salmon annual management report, 1999. Alaska Department of Fish and Game, Division of Commercial Fisheries, Kodiak, Regional Information Report No. 4K01-5.

2000: Jeff A. Wadle. 2001. Kodiak Management Area commercial salmon annual management report, 2000. Alaska Department of Fish and Game, Division of Commercial Fisheries, Kodiak, Regional Information Report No. 4K01-40.

2001: Kevin Brennan. 2001. Kodiak Management Area commercial salmon annual management report, 2001. Alaska Department of Fish and Game, Division

of Commercial Fisheries, Kodiak, Regional Information Report 4K01-62.

2002: Jeff A. Wadle. 2004. Kodiak Management Area commercial salmon annual management report, 2002. Alaska Department of Fish and Game, Division of Commercial Fisheries, Kodiak, Regional Information Report 4K04-01.

2003: Jeff A. Wadle. 2005. Kodiak Management Area commercial salmon annual management report, 2003. Alaska Department of Fish and Game, Division of Commercial Fisheries, Kodiak, Regional Information Report 4K05-1.

2004: Joe Dinnocenzo. 2006. Kodiak Management Area commercial salmon annual management report, 2004. Alaska Department of Fish and Game, Fishery Management Report No. 06-14 (March 2006), Anchorage. 194 p.

2005: Joe Dinnocenzo, Geoff Spalinger, and Jeff Wadle. 2006. Kodiak Management Area commercial salmon fishery annual management report, 2005. Alaska Department of Fish and Game, Fishery Management Report No. 06-53 (October 2006), Anchorage. 197 p.

2006: Joe Dinnocenzo, Geoff Spalinger, and Jeff Wadle. 2007. Kodiak Management Area commercial salmon fishery annual management report, 2006. Alaska Department of Fish and Game, Fishery Management Report No. 07-25 (April 2007), Anchorage. 188 p.

2007: Joe Dinnocenzo and Iris O. Caldentey. 2008. Kodiak Management Area commercial salmon fishery annual management report, 2007. Alaska Department of Fish and Game, Fishery Management Report No. 08-45 (September 2008), Anchorage. 178 p.

2008: Joe Dinnocenzo. 2010. Kodiak Management Area commercial salmon fishery annual management report, 2008. Alaska Department of Fish and Game, Fishery Management Report No. 10-02 (February 2010), Anchorage. 182 p.

2009: Joe Dinnocenzo, Geoff Spalinger, and Iris O. Caldentey. 2010. Kodiak Management Area commercial salmon fishery annual management report, 2009. Alaska Department of Fish and Game, Fishery Management Report No. 10-22 (May 2010), Anchorage. 188 p.

2010: James Jackson, Joe Dinnocenzo, and Geoff Spalinger. 2010. Kodiak Management Area commercial salmon fishery annual management report, 2010. Alaska Department of Fish and Game, Fishery Management Report No. 10-47 (December 2010), Anchorage. 184 p.

APPENDIX 5

Karluk River Sockeye Salmon Daily Escapements, 1921–2010

Day	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935	1936
10-May	—	—	—	—	—	—	—	0	0	—	—	—	—	—	—	—
11-May	—	—	—	—	—	—	—	0	0	—	—	—	—	—	0	0
12-May	—	0	—	—	—	—	0	0	0	—	—	—	—	—	0	0
13-May	—	0	—	—	—	—	0	0	0	—	—	0	—	—	0	0
14-May	—	0	—	0	—	0	0	0	0	—	0	0	0	—	0	0
15-May	—	0	—	0	—	0	0	0	0	—	0	0	0	—	0	0
16-May	—	0	—	1	—	0	0	0	0	—	0	0	0	—	0	0
17-May	—	0	—	0	—	0	0	0	0	0	0	0	0	—	0	6
18-May	—	0	—	32	0	0	0	0	0	0	0	0	0	—	0	1
19-May	—	0	—	12	0	0	0	0	11	7	0	0	0	—	0	7
20-May	—	7	—	9	0	32	0	0	0	0	0	0	0	—	0	7
21-May	—	0	0	0	0	0	0	0	0	9	0	0	145	—	0	5
22-May	—	0	0	73	0	0	0	0	1	0	0	10	57	0	3	0
23-May	—	53	0	179	19	18	0	10	8	70	0	16	67	195	0	6
24-May	—	0	141	96	0	527	0	31	2	922	1,250	8	14	683	4	0
25-May	—	231	313	193	485	327	1,180	2	26	141	1,804	12	6	722	21	26
26-May	167	82	252	170	528	433	1,617	97	11	347	2,110	184	1	702	111	33
27-May	366	0	339	531	829	159	2,427	56	2	458	1,063	71	42	136	5	1,415
28-May	180	12	28	597	1,734	34,286	4,142	163	0	6	4,860	206	146	5	5	2,440
29-May	1,654	14	101	287	10,475	22,110	140	1,595	43	0	972	43	673	2	18,731	16,498
30-May	2,346	2	19	437	2,250	9,208	29	1,523	90	5	376	167	651	7	1,089	13,813
31-May	1,181	77	50	1,934	13,698	14,181	4	10,164	666	171	157	404	582	57	3,037	4,335
1-Jun	601	117	61	2,136	6,317	49,289	13	11,365	3	457	103	684	478	60	5,605	6,273
2-Jun	2,035	468	24	1,221	18,927	96,444	0	6,320	1,625	117	419	1,775	9,060	10	16,711	36,813
3-Jun	2,906	261	165	3,261	2,694	55,580	0	199	12,730	743	238	643	6,138	111	21,838	26,274
4-Jun	3,479	2,473	159	5,082	2,652	48,506	9	1,226	23,371	5,052	1,007	248	5,455	113,421	9,652	17,381
5-Jun	1,144	2,747	1,791	5,869	1,799	92,947	0	726	6,007	11,749	8,516	12,404	1,866	64,308	25,763	23,107
6-Jun	2,244	2,101	47,006	26,919	292	81,317	58	51,789	9,398	14,816	17,621	16,826	598	14,218	13,788	15,533
7-Jun	3,845	1,754	22,518	41,623	52	55,372	52,452	80,744	22,242	9,418	22,478	15,611	986	9,418	45,510	18,827
8-Jun	1,746	472	4,868	29,384	1,775	88,788	65,241	75,238	3,964	4,467	30,943	14,117	1,268	11,943	60,346	13,371
9-Jun	4,034	414	2,933	20,560	2,685	79,962	45,148	69,346	3,419	1,823	17,753	50,099	2,335	4,129	21,572	20,186
10-Jun	11,814	323	300	24,406	954	57,381	29,249	32,361	744	1,112	25,908	7,534	7,578	17,975	37,081	18,060
11-Jun	8,456	178	673	22,947	2,578	80,946	12,352	50,164	1,096	69	10,742	4,212	23,988	3,536	20,359	14,624
12-Jun	44,102	1,157	1,536	14,712	2,480	42,371	12,769	1,213	11,179	162	9,467	26,535	46,788	38,128	17,068	3,699
13-Jun	48,753	2,204	3,937	25,341	3,027	29,750	21,367	29,440	16,401	414	6,984	29,018	75,960	64,200	14,657	8,935
14-Jun	36,192	3,607	14,596	11,067	6,941	57,853	25,067	46,214	48,544	13,761	7,250	18,543	46,097	29,805	1,643	14,284
15-Jun	13,132	8,247	1,603	13,266	1,415	41,245	19,367	9,104	25,837	18,416	11,930	2,184	23,623	21,942	3,611	13,659
16-Jun	17,566	24,276	5,889	24,325	38,403	58,057	2,181	19,697	42,748	43,265	5,015	167	17,864	31,161	7,246	18,493
17-Jun	7,442	6,709	6,570	17,214	79,534	20,881	2,276	7,035	18,698	56,103	2,463	16	10,093	66,489	6,517	17,450
18-Jun	22,600	7,024	1,600	20,158	66,437	4,592	76,848	15,307	4,903	48,779	1,891	33	15,683	15,216	14,186	11,167
19-Jun	39,560	3,603	8,742	16,180	42,395	1,718	36,875	18,257	2,395	31,856	520	0	3,693	44,488	21,435	5,627
20-Jun	12,854	3,548	11,877	25,488	18,063	323	36,577	14,153	4,032	23,762	5,165	0	3,900	47,512	5,156	7,597
21-Jun	24,180	3,332	5,888	11,014	16,782	721	14,654	13,968	17,829	6,224	7,610	0	9,984	6,818	6,098	8,707
22-Jun	18,103	4,611	19,395	8,190	30,031	1,277	25,109	12,660	10,216	4,315	6,826	0	13,904	21,302	6,529	10,962
23-Jun	27,145	1,535	15,245	9,833	32,873	9,146	23,117	13,958	6,718	4,435	1,832	0	14,628	19,003	2,198	13,679
24-Jun	59,443	1,733	3,505	16,774	58,951	5,432	23,593	17,525	3,023	6,916	5,889	0	11,880	13,827	1,559	4,466
25-Jun	27,882	2,000	6,329	7,553	42,406	4,547	10,557	17,489	8,001	8,168	14,335	0	3,382	15,760	3,491	7,186
26-Jun	25,646	2,373	8,868	8,240	21,890	6,230	710	9,115	9,584	982	6,909	9,414	6,351	16,689	1,234	10,928
27-Jun	19,497	9,386	6,472	7,914	16,993	5,713	1,097	1,749	5,642	6,807	1,294	1,346	4,562	16,471	9,136	17,802
28-Jun	17,435	8,259	3,140	6,409	7,877	13,175	827	2,743	6,986	3,395	1,828	4,178	10,514	15,115	7,293	14,267

Day	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935	1936
29-Jun	22,126	12,330	7,828	11,945	4,470	12,800	688	11,263	3,734	2,945	204	4,378	11,366	6,413	437	11,604
30-Jun	8,397	5,484	2,957	9,519	5,290	8,889	892	15,548	1,173	2,674	1,360	4,493	9,598	4,309	25	8,501
1-Jul	6,340	2,758	7,876	15,896	8,205	5,600	17,634	8,764	1,300	4,043	8,407	5,953	5,605	1,379	511	13,527
2-Jul	8,915	9,437	7,602	5,700	4,533	4,918	13,532	9,113	1,891	5,640	1,837	3,212	7,232	2,970	1,046	8,299
3-Jul	6,723	5,028	4,620	4,481	2,475	1,421	9,210	3,584	1,362	3,028	5,317	1,737	3,325	2,411	1,132	4,129
4-Jul	8,808	5,858	2,087	2,277	4,019	2,072	2,239	4,271	1,627	2,279	7,087	2,276	6,031	1,757	544	2,013
5-Jul	12,982	6,875	2,677	7,856	5,297	5,816	7,297	3,272	936	1,618	5,718	3,458	3,464	1,631	117	9,338
6-Jul	12,512	2,974	2,162	7,209	4,207	1,832	8,618	4,100	1,356	1,520	1,009	4,054	12,017	194	537	450
7-Jul	6,256	830	3,733	8,843	9,694	5,497	2,038	1,938	1,215	1,750	1,340	2,343	9,382	1,995	351	6,278
8-Jul	13,031	432	543	11,316	5,420	6,099	1,137	6,733	1,164	294	2,682	2,414	6,502	1,098	370	1,270
9-Jul	19,164	6,125	287	3,644	2,427	8,903	1,262	9,661	3,080	1,365	2,400	1,063	5,394	1,120	847	828
10-Jul	9,001	7,391	1,153	2,718	6,597	5,438	650	4,650	1,726	1,701	724	235	5,837	1,218	534	459
11-Jul	6,450	5,255	1,269	3,254	6,698	8,100	118	4,227	803	1,671	162	482	11,488	106	307	1,822
12-Jul	6,142	1,359	127	2,853	4,884	7,470	142	3,374	1,062	1,763	800	420	11,045	1,017	162	271
13-Jul	3,870	4,246	296	692	2,672	9,103	390	8,045	539	1,093	1,262	1,000	5,741	58	118	460
14-Jul	5,135	3,141	325	1,649	4,118	8,994	179	1,633	2,173	268	642	3,280	2,267	1,290	124	237
15-Jul	6,514	4,063	2,186	1,232	5,260	6,251	1,602	3,495	439	1,334	481	756	2,070	136	16	866
16-Jul	3,065	1,904	431	351	3,340	5,170	1,517	369	1,150	2,158	215	321	4,452	1,147	3	1,134
17-Jul	1,927	2,536	182	3,170	4,178	1,812	1,365	1,214	3,420	754	40	13	2,134	1,324	29	644
18-Jul	6,022	3,042	50	680	2,764	2,175	921	3,314	1,697	1,018	316	171	1,672	208	72	359
19-Jul	2,135	728	27	3,108	3,115	772	1,100	1,478	238	2,274	211	7	5,183	2,162	12	125
20-Jul	5,180	207	1,260	2,948	3,018	2,729	296	2,983	6	1,826	110	26	463	238	97	774
21-Jul	1,255	242	7,099	3,176	981	2,884	108	4,152	37	1,467	920	1,841	677	295	2,169	672
22-Jul	2,463	187	3,516	7,457	1,432	1,562	260	4,684	16	372	384	1,078	3,274	453	866	1,782
23-Jul	2,939	1,835	9,404	2,901	1,234	2,206	439	2,073	18	23	140	158	236	1,270	219	1,790
24-Jul	1,888	3,728	9,165	3,197	4,721	3,490	94	6,399	83	629	87	415	517	676	106	3,052
25-Jul	272	216	878	750	6,094	4,875	371	1,220	252	374	13	924	232	734	236	1,649
26-Jul	5,740	462	169	5,230	7,002	12,554	1,368	117	13	15	102	1,566	524	1,765	30	1,323
27-Jul	7,813	362	94	8,128	10,295	17,008	498	70	211	28	120	576	2,900	1,363	36	1,367
28-Jul	20,361	507	393	5,247	8,748	6,976	2,340	263	142	18	3,152	411	5,353	553	53	396
29-Jul	16,717	371	405	2,699	11,072	4,874	574	2,409	115	360	614	291	1,515	187	743	165
30-Jul	10,057	655	4,774	12,301	10,128	13,625	2,600	467	527	1,551	26	312	5,101	24	148	62
31-Jul	5,730	1,032	3,849	7,889	6,932	12,324	1,479	38	6,967	5,277	2,100	1,053	1,110	11	88	61
1-Aug	100	3,427	11,374	13,017	5,045	9,078	2,036	226	8,521	3,923	135	1,386	330	420	408	50
2-Aug	10,176	1,681	3,802	8,613	12,532	14,071	2,927	41	4,768	31,782	44	6,849	145	683	1,360	100
3-Aug	17,132	2,020	5,340	5,411	5,972	17,538	29,215	148	4,415	29,663	120	3,010	120	5,350	1,571	24
4-Aug	27,813	1,499	3,440	4,853	26,486	31,954	13,848	107	15,945	14,752	11	3,321	188	6,609	227	42
5-Aug	982	2,326	15,719	6,420	9,324	11,985	5,284	10,146	2,365	7,133	43	893	67	1,632	16	153
6-Aug	477	4,513	8,512	6,533	20,124	10,916	1,089	1,574	84	4,263	78	328	91	6,428	56	223
7-Aug	3,192	2,980	10,862	3,846	24,056	8,460	341	508	1,864	3,738	3,265	974	36,002	860	13,706	126
8-Aug	26,602	4,168	16,970	6,068	15,196	10,185	480	6,843	17	7,168	3,498	1,402	3,836	1,025	9,358	212
9-Aug	20,479	1,897	5,561	3,132	9,412	10,665	1,012	3,406	35	16,831	5,526	4,945	205	1,392	7,579	307
10-Aug	15,871	908	4,610	7,195	15,703	12,703	598	630	1,877	10,079	3,576	1,439	84	326	3,329	529
11-Aug	16,800	1,541	1,283	4,570	11,378	15,107	103	77	11,879	5,086	5,873	2,640	160	1,016	2,347	6,260
12-Aug	29,441	568	1,503	12,860	21,597	11,340	27	74	9,693	1,352	6,932	1,270	140	912	52	3,314
13-Aug	18,491	512	79	10,895	13,148	6,413	461	294	3,004	3,876	5,275	2,934	2,785	625	33	685
14-Aug	10,893	1,597	5,181	9,641	3,901	9,693	96	108	118	3,176	1,892	11,442	486	580	1,167	4,471
15-Aug	6,470	1,258	31	11,769	12,855	10,391	35	19,653	736	12,213	18,182	3,082	640	90	252	13,070
16-Aug	16,136	1,535	349	4,572	17,282	15,000	18,141	10,419	140	26,902	12,479	596	831	394	23,803	6,621

Day	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935	1936
17-Aug	7,030	2,681	3,359	2,905	7,209	13,162	3,335	193	171	13,567	5,138	139	553	83	23,661	6,242
18-Aug	1,386	1,411	5,011	5,745	2,147	39,880	328	56	0	6,260	18,967	952	695	618	674	22,221
19-Aug	34,213	1,147	18,584	14,791	4,618	16,161	400	156	15	1,886	1,240	1,794	188	394	14	6,684
20-Aug	12,926	356	12,753	23,904	141	6,480	55	50	64,804	13,195	4,607	3,503	6,040	2,626	10,155	6,616
21-Aug	639	0	2,653	7,012	1,076	1,827	708	68	3,958	38,605	38,930	770	41,660	2,126	4,541	789
22-Aug	2,112	0	4,321	—	3,118	18,174	1,441	21,365	204	19,498	5,477	1,038	501	0	317	652
23-Aug	561	0	1,930	—	1,396	8,465	1,156	49,127	58	5,480	630	681	135	0	13,151	1,247
24-Aug	7,456	0	552	—	256	28,449	130	23,005	0	6,004	8	936	254	0	18,090	43,136
25-Aug	13,278	0	3,743	—	212	38,427	16	7,518	0	158	0	808	97	0	635	9,779
26-Aug	10,244	0	4,997	—	5,110	19,395	7,158	951	0	0	20,518	2,057	39	0	156	1,671
27-Aug	7,959	0	819	—	234	31,813	935	386	0	0	42,603	3,164	154	0	248	1,628
28-Aug	55	0	2,100	—	135	9,258	185	435	43,067	0	40,072	1,409	45	0	29	40,974
29-Aug	61	0	15,241	—	8,441	55,174	22	27,408	21,656	0	2,432	2,639	95,063	0	31	15,590
30-Aug	40,263	0	11,015	—	19,409	42,076	10	8,154	4,829	0	729	1,528	5,238	0	382	17,804
31-Aug	31,286	0	201	—	20,185	30,115	6	5,816	79	67	8,941	4,029	2,456	0	78	59,978
1-Sep	1,418	0	1,484	—	1,933	31,500	20	143	0	80	12,419	1,745	1,677	300,000	808	142,182
2-Sep	117	0	7,802	—	39,444	58,660	13	1,719	35,293	56,812	40,065	8,292	160	0	4,996	60,714
3-Sep	22	0	409	—	2,065	21,492	7	172	254	32,607	19,645	10,444	2,555	0	2,697	19,467
4-Sep	115	0	4	—	74	12,523	12,377	625	30	7,038	2,227	1,306	4,576	0	112	5,283
5-Sep	9,134	197	14	—	126,754	49,228	2,443	11,095	237	1,490	18	1,949	16	0	2,012	3,441
6-Sep	882	41	18,005	—	9,794	26,960	826	393	67	20,876	45	297	2,778	0	1,928	852
7-Sep	12,509	174	37,586	—	776	9,275	9,510	2,013	598	37,411	40,410	82	10,089	0	20,128	202
8-Sep	9,402	941	3,424	—	2,535	28,103	198	12,150	459	11,892	9,254	33	14,873	0	19,041	484
9-Sep	41,040	507	58	—	3,639	13,105	73	793	0	9,820	710	20	1,937	0	2,620	634
10-Sep	49,000	313	16,391	—	8,366	24,643	12	2,271	32	3,461	16,845	24	4,884	0	37,360	44,279
11-Sep	28,562	550	3,834	—	2,044	9,397	207	65	68,294	8	20,630	11	5,008	0	22,694	6,115
12-Sep	2,222	17,065	67	—	15,459	2,134	0	5,091	30,721	15	21,247	26	12,243	0	46,019	60,324
13-Sep	287	4,793	29	—	41,911	4,479	7	208	9,812	2,785	12,368	1,582	6,843	0	3,189	92,942
14-Sep	701	1,617	13,208	—	14,130	229	12,961	852	12,407	23,173	2	77	3,783	0	110	24,967
15-Sep	11,370	16,247	25,291	—	9,765	27,011	134	2,656	5,776	13,794	0	104	4,839	0	22	845
16-Sep	2,324	9,531	2,318	—	2,952	43,000	37	94	44,162	5,623	0	11	4,788	0	43	177
17-Sep	291	6,049	235	—	13,771	8,396	130	72	20,339	338	0	52,956	17,658	0	22	534
18-Sep	74	1,476	1,055	—	55	14,000	18,459	6,683	6,149	0	9	26,558	382	509	64	113
19-Sep	2,650	339	39	—	2,340	32,428	8,421	2,860	1,594	186	16	7,446	7	175	70	65
20-Sep	276	359	1,071	—	57,418	31,875	3,103	1,712	3,401	12,471	88	633	11	635	22	1,048
21-Sep	146	34	1,259	—	13,759	7,041	246	780	2,024	19,853	42,615	39	0	18	5	3,090
22-Sep	112	4	392	—	2,366	2,450	44	1,589	2,847	60,110	19,685	4	3	1,139	0	9,162
23-Sep	252	16	43	—	9,579	14,338	401	2,185	5,690	55,163	1,740	87,474	3	763	36	2,475
24-Sep	633	0	8,464	—	5,197	1,354	183	844	1,468	316	102	29,272	0	281	84,877	825
25-Sep	257	0	200	—	3,074	16,786	208	1,072	1,687	15	59	2,822	5	566	4,137	37,346
26-Sep	0	7	185	—	7,853	3,581	102	1,001	204	11	293	172	107	265	24,223	28,037
27-Sep	143	0	27	—	9,987	4,059	110	0	80	0	107	299	1,767	40,020	1,971	221
28-Sep	1,965	12	29	—	51,351	3,000	16	3	347	7	17	2,283	3,422	280	92	846
29-Sep	11,931	0	1,008	—	27,974	270	7	80	5,683	2	46	401	436	20	105	4,219
30-Sep	0	27	7,354	—	4,452	1,010	0	45	10,532	0	80	70	179	41	2,285	6,347
1-Oct	4,882	33	21,904	—	34,166	2,660	26,050	15	36,071	15	137	9	5	60	9,479	610
2-Oct	9,742	220	5,682	—	57,055	1,796	12,000	15	9,842	119	29,891	297	0	15	2,766	87
3-Oct	4,472	12,756	22,906	—	4,811	444	2,736	0	10,138	1,054	10,650	12,911	14	18	2,311	1,121
4-Oct	8,335	2,673	3,758	—	2,964	268	31,750	0	154	291	850	31,107	0	192	281	1,392
5-Oct	32,003	32	3,800	—	4,385	25	5,013	0	32	1,093	100	10,151	12	17	11	361

Day	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935	1936
6-Oct	0	48	1,453	—	234	124	1,554	561	43	2,218	4,226	—	5	—	—	0
7-Oct	1,731	32	593	—	—	21	2,985	0	70	23,436	6,967	—	1,670	—	—	0
8-Oct	2,134	8,294	476	—	—	417	777	106	0	17,974	134	—	38,529	—	—	—
9-Oct	1,308	17,179	11	—	—	12,140	162	398	0	0	—	—	17,324	—	—	—
10-Oct	1,451	3,231	44	—	—	17,127	0	50	0	—	—	—	—	—	—	—
11-Oct	4,600	300	2,733	—	—	13,460	0	44,867	0	—	—	—	—	—	—	—
12-Oct	2,308	0	1,683	—	—	7,574	0	8,778	0	—	—	—	—	—	—	—
13-Oct	6,216	7,141	—	—	—	8,307	0	296	0	—	—	—	—	—	—	—
14-Oct	1,833	16,328	—	—	—	7,264	—	—	0	—	—	—	—	—	—	—
15-Oct	676	11,103	—	—	—	—	—	—	—	—	—	—	—	—	—	—
16-Oct	57	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—
17-Oct	21	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—
18-Oct	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—
19-Oct	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—
20-Oct	122	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—
21-Oct	3,280	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—
22-Oct	4,081	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—
23-Oct	6,156	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—
24-Oct	1,653	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—
25-Oct	407	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—
26-Oct	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
27-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
28-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
TOTAL	1,441,498	384,684	694,580	775,705	1,620,691	2,513,392	874,870	1,090,961	899,506	1,091,063	866,428	630,290	896,563	1,146,279	876,335	1,355,661

Day	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952
10-May	—	0	—	—	—	0	—	—	—	—	—	—	—	—	—	—
11-May	—	0	—	—	—	0	—	—	—	—	—	—	—	—	—	—
12-May	—	0	—	—	—	0	—	—	—	—	—	—	—	—	—	—
13-May	—	0	—	—	—	0	—	—	—	—	—	—	—	—	—	—
14-May	—	0	—	—	—	0	—	—	—	—	—	—	—	—	—	—
15-May	—	0	—	—	—	0	—	—	—	—	—	—	—	—	—	—
16-May	—	0	—	—	—	0	—	—	—	—	—	—	—	—	—	—
17-May	0	0	—	—	—	2	—	—	—	—	—	—	—	—	—	—
18-May	0	0	—	—	—	225	—	—	—	—	—	—	—	—	—	—
19-May	0	11	0	0	—	257	—	—	—	—	—	—	—	—	—	—
20-May	0	4	0	0	—	1,734	—	—	—	—	—	0	—	0	—	—
21-May	0	6	1	5	—	833	—	—	—	—	—	3	—	0	—	—
22-May	0	2	0	0	—	327	—	—	—	—	—	0	0	0	—	—
23-May	0	3	0	0	3	550	—	—	—	—	—	22	9	0	—	—
24-May	0	6	0	0	0	2,280	—	—	—	—	—	1	42	0	—	—
25-May	0	2	12	0	2	5,545	—	0	—	—	—	0	96	0	—	0
26-May	0	1	39	2,477	11	4,489	—	0	—	—	0	10	127	0	—	0
27-May	9	7	42	3,145	2	8,003	—	0	—	—	18	117	234	0	0	0
28-May	5	40	23	5,125	78	5,512	—	0	—	—	49	4	277	8	0	12
29-May	0	2	9	74,212	1,495	3,460	—	14	0	—	95	8	57	83	0	2
30-May	7	2	18	29,672	18,819	5,396	—	47	5	—	41	7	219	47	0	19
31-May	0	2	18	35,339	5,717	1,845	0	36	30	—	100	368	66	203	0	19
1-Jun	28	0	128	21,689	41,102	1,368	0	46	42	—	151	11	203	446	380	25
2-Jun	103	6	52	3,992	80,300	2,054	0	3	37	—	3	4	121	391	380	30
3-Jun	0	0	53	16,423	19,847	11,452	13,502	7,989	48	0	692	10,733	668	1,435	380	24
4-Jun	29	0	9,549	12,867	16,107	15,797	6,211	36,658	9,375	23	15	21,034	54	749	2,618	2
5-Jun	0	21	5,316	17,905	8,476	16,859	9,005	8,598	15,763	63	34	15,653	50	212	1,447	34
6-Jun	22	2	43,928	27,669	33,864	15,492	3,194	4,235	4,480	300	936	13,393	245	263	3,736	214
7-Jun	5,005	89	24,467	18,747	433	11,717	5,924	1,312	718	1,905	48	7,505	102	518	3,586	503
8-Jun	6,873	63,621	8,339	17,018	8,096	10,758	7,890	1,234	725	4,339	918	8,533	609	18,038	4,562	1,853
9-Jun	168	68,595	36,068	57,420	4,687	16,530	45,363	935	1,887	15,867	220	21,692	11,316	10,050	6,999	1,328
10-Jun	115,290	37,602	12,778	22,467	9,774	10,305	38,608	794	7,332	24,673	251	51,777	14,654	6,252	3,408	11,495
11-Jun	88,763	31,340	22,429	23,095	14,822	14,109	24,809	37,447	19,876	17,491	1,984	27,945	5,341	9,716	304	1,981
12-Jun	63,499	16,914	15,505	6,287	4,724	11,828	25,832	39,557	11,789	8,343	2,607	22,973	9,086	12,714	1,621	5,505
13-Jun	51,915	31,535	15,355	24,199	18,444	6,656	18,652	18,037	26,820	9,950	325	41,522	17,448	7,238	5,158	7,379
14-Jun	14,307	34,053	10,483	7,585	18,511	7,419	25,244	9,883	36,341	18,653	6,540	36,481	24,656	3,198	29,245	16,352
15-Jun	20,727	68,895	9,787	19,377	4,272	7,755	27,501	18,589	28,950	16,241	25,024	28,544	39,834	2,663	23,946	30,161
16-Jun	8,981	22,500	4,007	13,390	5,003	10,865	14,389	14,154	31,746	11,334	7,290	16,158	15,356	4,273	10,984	40,305
17-Jun	3,621	27,091	4,166	22,671	8,333	10,501	9,904	8,465	16,162	4,983	3,593	26,716	15,826	10,539	15,257	34,032
18-Jun	103,605	83,102	4,649	14,969	7,051	7,449	23,361	12,372	11,498	2,132	11,740	27,561	7,154	15,841	3,428	15,836
19-Jun	28,238	47,098	11,088	5,130	3,852	8,367	30,324	17,954	20,854	3,954	6,725	19,047	26,747	34,318	1,336	13,192
20-Jun	90,993	33,448	6,034	3,272	3,711	7,734	11,219	13,339	20,114	2,982	15,826	12,664	45,770	21,486	1,619	11,007
21-Jun	39,281	57,287	2,407	4,270	3,680	7,502	14,158	10,118	32,142	3,012	14,675	11,677	27,007	24,318	828	4,876
22-Jun	26,862	43,396	7,225	11,593	1,114	11,767	17,498	11,865	19,482	10,712	12,854	14,425	11,663	24,455	2,616	7,280
23-Jun	20,506	29,256	13,003	7,101	3,739	12,031	22,085	7,226	14,035	29,357	7,025	14,112	8,536	19,375	9,614	5,749
24-Jun	13,158	13,748	24,672	8,764	6,381	7,311	26,945	5,079	11,969	25,047	12,333	10,216	11,267	17,316	22,404	5,537
25-Jun	41,391	2,360	11,394	11,158	5,224	5,449	18,789	6,797	12,062	13,553	7,676	12,056	7,736	13,210	22,286	2,537
26-Jun	21,600	6,847	11,280	3,940	3,411	3,224	18,902	6,238	14,287	6,658	8,272	9,374	3,682	5,354	17,194	5,536

Day	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952
27-Jun	20,383	7,068	9,553	4,500	1,077	3,232	12,479	9,064	12,456	10,938	6,991	7,862	5,820	6,628	12,136	5,770
28-Jun	9,214	5,010	5,330	2,004	927	2,074	20,078	6,173	14,096	7,140	11,428	9,646	4,445	9,808	6,692	5,404
29-Jun	7,846	7,635	4,292	4,163	3,343	2,139	13,109	7,190	8,502	7,564	6,767	6,339	4,563	18,994	4,422	6,831
30-Jun	5,374	4,755	3,324	4,816	2,605	3,339	13,097	5,392	2,216	8,483	8,106	8,448	8,078	18,564	3,253	5,143
1-Jul	8,571	3,097	2,683	2,783	2,403	3,775	19,373	4,876	5,093	6,158	7,390	5,720	6,931	13,189	3,062	5,172
2-Jul	5,343	3,137	2,280	1,228	6,055	5,646	11,027	3,535	2,385	4,569	5,361	3,370	5,068	4,132	2,005	2,216
3-Jul	4,541	7,313	2,016	4,041	5,392	1,979	7,954	2,539	3,130	3,892	5,817	4,001	5,432	5,696	1,328	6,180
4-Jul	804	3,743	2,990	1,560	2,131	1,113	3,689	1,279	3,000	3,547	6,312	3,150	7,364	3,222	2,975	4,310
5-Jul	403	5,262	2,081	1,653	1,711	3,886	4,129	2,718	1,715	2,342	3,285	1,905	4,815	6,141	2,709	4,479
6-Jul	9,457	7,054	2,970	2,218	477	931	9,224	1,485	1,252	2,578	4,623	2,226	3,728	5,221	3,657	2,605
7-Jul	9,138	3,529	2,259	1,392	1,312	1,388	7,884	1,639	2,032	1,863	4,172	2,525	3,106	4,502	2,981	2,139
8-Jul	837	3,142	1,316	1,281	4,304	4,062	3,996	783	2,273	2,075	2,485	1,975	1,470	3,346	1,725	2,377
9-Jul	12,535	4,631	2,474	1,982	2,212	1,805	4,853	279	2,113	1,479	2,053	2,614	1,146	2,661	1,969	1,873
10-Jul	270	836	2,416	3,019	4,474	1,581	5,278	1,065	1,481	2,226	2,418	1,419	1,212	1,469	1,486	1,602
11-Jul	1,159	1,872	1,505	1,985	1,717	1,352	3,462	523	1,399	1,516	1,168	1,813	924	1,092	1,023	1,251
12-Jul	4,941	5,360	1,417	1,820	362	1,692	2,025	203	907	1,593	1,695	855	477	2,557	860	2,155
13-Jul	2,724	7,689	1,442	700	1,465	2,376	1,708	167	994	1,332	1,779	370	1,064	1,035	692	1,674
14-Jul	349	2,121	1,305	297	2,640	1,541	4,056	323	1,620	858	1,187	887	1,622	972	538	869
15-Jul	4,564	2,494	961	397	1,046	1,921	4,455	15	1,456	833	460	1,483	923	434	264	1,327
16-Jul	1,026	3,836	1,474	74	307	1,057	1,952	392	1,917	929	1,097	1,677	636	778	669	888
17-Jul	300	1,273	1,454	103	605	792	2,186	612	1,077	954	572	1,215	575	92	188	1,291
18-Jul	305	2,437	1,435	44	234	1,154	1,505	311	1,560	980	394	1,145	594	1,341	1,557	541
19-Jul	432	1,821	723	10	510	593	645	6	1,312	1,271	684	1,385	771	494	1,587	582
20-Jul	118	1,567	756	512	411	512	25	34	1,990	1,797	1,077	953	764	336	556	1,504
21-Jul	794	1,677	85	195	1,505	1,149	80	363	2,228	1,898	918	473	936	511	1,215	1,027
22-Jul	350	2,099	957	155	2,308	491	510	37	1,829	959	815	862	1,085	1,010	1,054	1,017
23-Jul	52	1,126	332	280	201	945	196	4	2,638	349	199	1,397	1,592	546	1,392	890
24-Jul	2,638	916	858	289	56	932	736	85	2,737	1,154	836	1,020	459	585	1,864	282
25-Jul	537	132	835	1,642	102	155	110	187	1,754	704	609	608	1,189	1,295	1,296	707
26-Jul	275	4,837	1,338	3,032	347	2,956	160	262	470	919	404	928	819	815	2,701	753
27-Jul	2,548	923	920	1,521	160	1,278	844	969	1,793	531	112	1,744	1,829	1,251	1,607	803
28-Jul	3,064	876	4,261	1,518	245	999	235	624	1,646	950	62	883	1,066	919	3,450	920
29-Jul	2,057	132	397	334	256	695	1,227	262	1,680	275	200	360	1,181	2,143	6,166	313
30-Jul	1,451	24	69	182	12,738	81	1,331	1,793	2,531	215	219	2,889	783	1,322	6,687	71
31-Jul	199	744	375	147	7,085	163	334	3,475	2,667	347	2,323	2,734	730	1,516	4,546	695
1-Aug	91	718	637	188	3,457	132	750	2,838	6,558	840	2,194	3,002	1,129	1,314	1,459	513
2-Aug	2,043	648	3,049	80	713	79	932	3,977	3,266	554	2,607	2,126	1,883	482	6,049	431
3-Aug	1,689	3,081	7,850	158	3,847	190	1,856	4,384	3,185	351	2,713	2,908	1,944	621	5,469	619
4-Aug	0	3,548	14,334	769	2,529	323	395	1,873	3,403	86	598	3,833	4,822	1,384	1,905	907
5-Aug	1,618	2,107	912	349	13,548	815	412	4,419	1,940	554	3,622	2,505	6,155	1,232	8,414	506
6-Aug	0	1,529	596	702	163	174	26	1,730	4,355	526	3,264	1,308	3,783	2,876	11,291	411
7-Aug	443	2,754	1,408	2,123	148	2,833	428	3,210	9,905	428	3,115	2,787	3,116	8,541	7,754	440
8-Aug	304	2,191	1,207	1,160	2,062	173	263	1,817	6,009	691	6,952	2,819	5,395	7,940	5,574	410
9-Aug	17,417	3,108	963	450	5,739	6,324	989	820	5,174	968	3,704	3,147	1,953	3,703	1,784	326
10-Aug	2,573	1,351	202	281	7,508	2,308	784	1,310	5,355	845	2,073	1,015	2,835	3,074	1,571	6
11-Aug	6,224	2,157	357	657	9,744	390	3,294	1,060	3,040	625	4,362	1,553	2,973	2,513	9,797	1
12-Aug	1,390	1,504	27,837	565	32,106	3,074	1,640	684	5,375	269	3,188	1,653	3,153	958	19,773	16
13-Aug	68	3,431	6,688	768	3,736	2,105	2,758	470	4,730	184	6,529	1,336	799	3,092	5,672	16

Day	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952
14-Aug	148	1,977	476	1,143	6,264	4,147	1,347	2,544	4,840	136	2,969	2,147	2,778	2,368	1,656	8
15-Aug	87	1,118	30	1,240	4,482	1,695	1,962	3,013	2,960	279	4,986	1,867	6,471	3,966	7,834	6
16-Aug	269	2,274	42	3,503	3,893	2,715	3,269	4,340	1,618	37	7,016	5,326	11,479	4,602	6,091	46
17-Aug	4,155	1,572	22	5,420	2,687	752	3,281	5,730	4,115	76	9,139	9,074	13,176	4,127	4,289	95
18-Aug	490	763	407	685	3,303	4,814	896	3,508	6,656	188	6,174	9,256	11,219	2,605	2,499	101
19-Aug	401	676	41	721	4,898	1,797	833	1,608	4,148	69	5,672	2,848	6,851	4,270	5,384	300
20-Aug	795	725	73	915	4,020	2,084	187	1,426	1,644	83	5,797	3,384	4,466	2,032	2,873	0
21-Aug	96	893	123	480	587	6,674	12	3,211	2,315	185	7,208	2,428	5,051	1,228	3,554	227
22-Aug	36	1,531	162	1,106	224	1,399	3,174	1,021	1,265	200	4,186	5,673	4,718	589	4,484	518
23-Aug	21,202	876	2,083	441	35	2,356	405	2,041	2,359	119	3,757	3,366	5,307	1,082	428	308
24-Aug	5,043	1,052	683	682	403	4,425	4,271	2,717	850	168	3,418	2,385	2,569	935	2,367	139
25-Aug	116	989	196	0	1,651	3,846	5,772	4,230	4,333	52	3,713	2,258	4,254	418	5,907	241
26-Aug	25	342	471	—	2,843	12,041	10,990	3,251	3,337	83	6,290	8,186	2,160	614	9,180	312
27-Aug	240	275	277	—	981	3,826	4,631	2,874	1,742	29	2,985	3,187	12,696	420	4,026	611
28-Aug	3,117	329	1,278	—	356	4,862	3,156	1,290	2,683	61	5,255	3,123	16,286	489	19,419	807
29-Aug	18,465	704	19,799	—	4,224	4,287	185	1,830	1,620	128	10,419	4,480	11,013	2,106	22,009	1,825
30-Aug	939	964	1,537	—	1,972	3,877	155	2,037	2,117	64	9,745	3,345	6,823	5,921	15,617	16,005
31-Aug	69	658	167	—	5,344	4,000	694	1,580	706	191	7,210	2,705	4,922	13,259	2,898	22,946
1-Sep	8,567	461	42,440	—	7,297	4,000	4,954	—	395	138	5,288	1,159	20,240	6,794	2,350	26,460
2-Sep	3,624	289	1,224	—	10,089	4,000	8,661	—	211	194	2,456	425	7,557	6,924	2,312	17,501
3-Sep	5,748	312	313	—	17,988	4,000	1,028	—	2,709	293	5,591	477	2,333	3,368	1,373	16,333
4-Sep	21,068	3,409	128	—	12,207	4,000	23,183	—	3,668	502	6,599	886	2,777	3,658	2,109	14,977
5-Sep	21,908	3,409	39	—	6,152	1,880	8,368	—	1,827	154	4,296	10,416	3,183	4,041	1,545	9,011
6-Sep	118	3,409	65,431	—	1,585	4,088	1,498	—	1,128	61	1,596	12,472	1,068	6,172	2,632	4,615
7-Sep	1,378	3,409	23,255	—	299	6,760	448	—	2,068	41	3,560	4,775	2,354	16,238	494	3,599
8-Sep	16,589	3,409	3,560	—	26,684	4,139	1,472	—	8,571	77	2,530	3,289	1,608	30,257	436	3,650
9-Sep	128	3,409	2,213	—	43,468	3,815	1,636	—	3,954	113	5,544	4,152	1,009	6,697	6,561	12,802
10-Sep	0	3,409	581	—	43,468	3,895	—	—	6,782	217	3,803	1,483	269	4,030	21,846	8,824
11-Sep	178	3,409	13,159	—	43,468	2,376	—	—	1,675	503	2,607	1,062	134	545	7,562	2,776
12-Sep	2,840	3,409	5,347	—	43,468	2,894	—	—	775	1,039	3,926	1,048	311	344	2,863	688
13-Sep	281	3,409	964	—	43,468	8,596	—	—	328	1,003	4,705	1,216	4,287	878	11,335	588
14-Sep	72	3,409	425	—	—	3,880	—	—	1,653	1,102	4,992	4,851	23,256	20,295	5,618	277
15-Sep	153	3,409	34	—	—	2,893	—	—	3,773	2,146	3,214	3,200	12,134	31,152	5,885	168
16-Sep	24,236	3,409	109	—	—	10,098	—	—	3,466	4,813	2,247	2,160	4,227	17,688	8,420	130
17-Sep	47,978	3,409	2,535	—	—	8,570	—	—	3,633	3,332	2,268	2,306	2,805	16,703	11,161	3,260
18-Sep	7,421	3,409	19,359	—	—	4,280	—	—	3,000	4,665	489	5,003	343	4,841	6,764	4,635
19-Sep	2,859	3,409	1,301	—	—	5,762	—	—	742	2,943	7,895	2,296	927	7,527	8,533	5,940
20-Sep	2,157	3,409	47	—	—	18,050	—	—	2,079	5,906	3,908	632	2,559	13,597	4,400	12,760
21-Sep	0	3,409	3,441	—	—	5,000	—	—	2,081	3,481	2,663	2,380	3,826	11,015	10,914	5,774
22-Sep	218	3,409	2,974	—	—	5,000	—	—	2,975	2,212	2,269	3,494	11,418	12,338	12,197	3,113
23-Sep	60	3,409	40,000	—	—	5,000	—	—	4,830	2,616	1,348	1,489	9,456	12,694	6,125	617
24-Sep	2,486	3,409	—	—	—	5,000	—	—	5,181	3,253	727	582	5,351	10,026	6,930	532
25-Sep	1,192	3,409	—	—	—	5,000	—	—	3,563	5,444	2,211	591	2,199	7,035	6,217	186
26-Sep	29	—	—	—	—	5,000	—	—	548	3,928	1,610	564	1,270	2,629	3,437	212
27-Sep	35	—	—	—	—	5,000	—	—	1,040	1,312	1,472	931	593	4,072	782	394
28-Sep	27,090	—	—	—	—	5,000	—	—	1,138	2,004	372	733	1,530	3,337	3,416	305
29-Sep	18,486	—	—	—	—	5,000	—	—	1,507	6,154	427	2,879	—	2,189	1,128	341
30-Sep	6,628	—	—	—	—	5,000	—	—	1,062	1,056	625	1,031	—	1,216	1,838	4,484

Day	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952
1-Oct	18,177	—	—	—	—	4,206	—	—	949	3,030	193	449	—	1,951	1,572	25,245
2-Oct	5,611	—	—	—	—	3,785	—	—	924	2,473	315	564	—	1,924	1,986	12,708
3-Oct	679	—	—	—	—	4,562	—	—	396	2,323	45	495	—	1,983	1,317	3,773
4-Oct	5,937	—	—	—	—	3,862	—	—	552	3,426	—	—	—	1,533	2,560	891
5-Oct	0	—	—	—	—	4,138	—	—	851	7,161	—	—	—	1,135	1,357	315
6-Oct	5,923	—	—	—	—	2,781	—	—	340	3,441	—	—	—	896	154	93
7-Oct	—	—	—	—	—	685	—	—	88	1,450	—	—	—	391	1,102	12
8-Oct	—	—	—	—	—	1,206	—	—	66	10,444	—	—	—	302	163	—
9-Oct	—	—	—	—	—	271	—	—	102	14,132	—	—	—	49	1,023	—
10-Oct	—	—	—	—	—	103	—	—	109	4,281	—	—	—	2,000	1,369	—
11-Oct	—	—	—	—	—	162	—	—	—	1,833	—	—	—	—	878	—
12-Oct	—	—	—	—	—	1,738	—	—	—	2,274	—	—	—	—	37	—
13-Oct	—	—	—	—	—	641	—	—	—	344	—	—	—	—	14	—
14-Oct	—	—	—	—	—	302	—	—	—	355	—	—	—	—	15,000	—
15-Oct	—	—	—	—	—	209	—	—	—	424	—	—	—	—	—	—
16-Oct	—	—	—	—	—	—	—	—	—	120	—	—	—	—	—	—
17-Oct	—	—	—	—	—	—	—	—	—	194	—	—	—	—	—	—
18-Oct	—	—	—	—	—	—	—	—	—	64	—	—	—	—	—	—
19-Oct	—	—	—	—	—	—	—	—	—	127	—	—	—	—	—	—
20-Oct	—	—	—	—	—	—	—	—	—	0	—	—	—	—	—	—
21-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
22-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
23-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
24-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
25-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
26-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
27-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
28-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
TOTAL	1,238,992	950,967	705,993	629,436	866,916	627,685	734,256	434,528	658,860	444,457	484,729	753,747	690,658	758,551	688,390	555,572

Day	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968
10-May	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
11-May	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
12-May	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
13-May	—	—	0	—	—	—	—	—	—	—	—	—	—	—	—	—
14-May	—	—	0	—	—	—	—	—	—	0	—	—	—	—	—	—
15-May	—	—	0	—	0	—	—	—	—	0	—	—	—	—	—	—
16-May	—	—	0	—	0	—	—	—	—	1	—	—	—	—	—	—
17-May	—	—	0	—	0	—	—	—	—	0	—	—	—	—	—	—
18-May	0	—	0	—	0	—	—	—	—	2	—	—	—	—	—	—
19-May	0	—	0	—	0	—	—	—	—	4	—	—	—	—	—	—
20-May	0	0	0	0	0	—	—	—	—	0	—	—	—	—	—	—
21-May	0	0	0	0	0	—	—	—	—	0	0	0	—	—	—	—
22-May	0	0	0	0	0	—	—	—	0	0	1	2	—	—	—	—
23-May	35	0	2	0	0	—	—	—	0	3	4	0	—	—	—	—
24-May	13	4	26	0	26	—	—	—	0	1	1	0	—	0	—	—
25-May	68	6	35	0	9	—	—	—	0	4	0	0	—	1	—	—
26-May	22	6	36	0	0	—	—	—	9	10	3	7	—	0	0	—
27-May	59	7	10	0	0	—	—	—	32	0	1	0	—	0	1	—
28-May	116	39	22	14	27	—	—	0	17	2	1	3	0	0	0	—
29-May	485	24	14	31	45	—	—	15	174	23	0	1	1	0	2	—
30-May	361	28	13	8	125	—	—	13	133	31	1	0	0	14	0	0
31-May	112	7	5	6	74	6	0	21	138	5	38	45	0	0	0	2
1-Jun	172	16	26	3	0	414	0	363	1,226	210	52	8	3	0	0	0
2-Jun	405	247	10	8	256	750	39	16	487	32	4	44	1	20	109	0
3-Jun	296	124	0	26	200	1,908	379	128	390	183	1	36	2	0	0	27
4-Jun	43	208	6	76	445	2,526	330	61	48	178	817	154	1	438	64	0
5-Jun	57	352	94	32	1,984	1,782	74	64	308	264	1,761	623	0	0	148	0
6-Jun	306	158	137	20	2,950	4,632	1,335	149	345	16	1,577	223	4	125	122	541
7-Jun	1,997	558	121	172	4,091	1,914	3,080	3,795	161	956	1,207	1,084	1	122	4,716	15
8-Jun	11,869	859	35	416	3,726	2,580	292	5,325	498	459	792	1,466	1	845	22	6
9-Jun	4,862	363	0	127	3,075	288	255	1,629	817	303	1,688	3,752	3	496	2,531	4,634
10-Jun	3,649	2,007	5	275	3,060	1,038	2,482	1,763	1,747	1,262	2,029	1,388	1	1,018	4,790	174
11-Jun	3,395	2,785	792	18	1,176	366	4,252	1,022	6,550	7,813	4,240	1,515	10	59	4,579	7,196
12-Jun	3,382	16,224	631	106	757	1,998	3,855	3,804	16,171	8,061	751	3,007	431	2,936	3,278	5,962
13-Jun	3,781	8,677	768	7	3,491	2,220	38,409	2,365	9,302	8,995	4,181	7,662	141	8,717	5,525	7,053
14-Jun	1,082	5,268	1,749	0	4,013	600	6,278	2,222	384	4,227	3,532	5,105	294	8,530	3,524	3,926
15-Jun	6,427	4,381	14,575	1,278	3,496	336	2,602	3,110	12,242	12,811	17,465	6,944	49	2,792	6,068	1,976
16-Jun	13,813	4,865	8,116	75	4,062	618	3,032	1,407	5,251	7,733	9,154	4,200	2,323	1,045	12,003	4,919
17-Jun	32,627	3,760	23,728	23	2,679	276	10,767	5,146	7,915	10,500	11,417	11,145	4,714	2,362	12,930	7,477
18-Jun	25,962	9,643	10,612	468	2,353	2,856	11,626	4,566	10,724	12,941	11,741	6,227	2,956	1,734	10,251	6,340
19-Jun	26,858	18,922	4,947	200	4,452	3,942	3,348	7,181	9,696	10,755	12,316	8,155	114	706	4,833	14,454
20-Jun	33,383	24,430	12,525	569	4,806	4,572	3,923	10,195	6,507	8,564	9,431	5,851	1,017	1,466	7,913	10,940
21-Jun	27,468	13,318	7,655	974	3,361	2,808	2,453	9,188	6,946	8,145	6,525	6,491	1,334	8,967	6,714	7,897
22-Jun	15,028	3,092	8,024	10,728	1,860	2,964	4,732	7,180	4,646	5,864	3,528	9,155	556	3,074	5,824	9,014
23-Jun	7,450	7,147	5,592	5,665	2,106	2,628	9,128	4,350	6,281	8,910	3,134	8,280	2,300	7,207	3,668	6,103
24-Jun	9,755	6,630	5,875	5,223	2,294	3,612	3,492	5,122	3,444	4,875	2,228	13,300	1,188	2,972	2,910	8,803
25-Jun	9,527	10,201	6,229	4,817	2,967	2,898	3,053	2,110	3,957	6,061	4,549	11,752	11,150	3,285	4,034	7,687
26-Jun	5,745	9,126	4,319	2,976	3,061	4,612	5,071	1,480	5,991	6,867	4,374	3,061	5,128	2,564	3,684	6,909

Day	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968
27-Jun	3,492	4,373	4,076	3,517	1,901	4,548	3,285	1,002	5,129	7,225	6,767	17,751	4,018	4,054	6,393	6,214
28-Jun	4,122	2,037	5,798	5,083	1,730	2,982	1,672	916	4,658	4,634	7,176	4,229	1,434	3,069	5,372	4,510
29-Jun	3,258	1,487	4,630	7,772	1,580	1,422	1,012	264	2,907	9,045	4,872	3,312	770	145	5,619	6,634
30-Jun	1,200	1,553	4,154	2,603	576	1,764	2,332	1,435	3,996	6,770	5,465	6,169	2,709	8,096	5,487	2,828
1-Jul	4,624	2,449	4,180	1,215	1,673	2,060	2,032	1,400	4,097	6,455	3,538	1,116	1,450	659	2,730	2,623
2-Jul	2,747	1,665	5,694	1,497	1,624	1,632	1,897	681	3,139	4,800	3,784	5,559	3	333	2,214	2,476
3-Jul	2,403	1,494	4,405	2,929	2,013	1,008	1,050	715	2,372	5,630	1,642	2,233	2,829	2,740	2,402	971
4-Jul	1,456	1,292	2,553	1,476	1,376	2,202	2,962	590	1,872	9,800	1,287	2,939	627	728	1,727	995
5-Jul	1,641	1,789	2,832	1,280	1,155	1,806	438	991	2,227	6,455	3,128	2,076	3,003	798	1,759	537
6-Jul	1,898	636	1,412	1,086	1,290	924	2,432	480	2,049	3,945	1,339	4,122	1,414	1,127	1,272	391
7-Jul	1,106	1,315	1,066	1,061	698	474	1,830	201	1,634	3,540	1,766	466	727	2,467	1,389	773
8-Jul	931	1,142	393	746	989	786	3,473	601	1,640	2,785	632	4,477	2,000	448	813	56
9-Jul	816	1,034	1,065	204	707	348	1,957	554	1,182	2,168	650	4,005	308	1,254	1,615	556
10-Jul	1,245	871	893	320	894	786	1,363	115	1,386	3,170	1,156	1,925	222	1,200	997	72
11-Jul	592	672	704	509	699	420	1,738	870	1,140	2,197	1,026	1,000	438	976	730	75
12-Jul	622	708	550	224	472	576	922	1,058	778	1,444	960	3,457	1,056	764	1,222	97
13-Jul	734	799	568	543	407	354	640	1,336	795	342	840	1,400	16	631	1,019	1,057
14-Jul	841	588	410	261	310	234	1,500	747	952	923	320	2,005	27	485	428	116
15-Jul	967	186	606	241	192	330	1,477	408	990	1,330	1,120	1,000	2,520	237	997	266
16-Jul	83	326	518	410	162	150	1,155	362	474	1,711	735	250	2,443	143	347	51
17-Jul	1,035	177	427	212	103	126	51	499	733	1,940	86	213	49	237	1,193	765
18-Jul	693	211	51	697	87	174	312	803	151	925	15	350	227	1,035	296	443
19-Jul	280	152	478	360	173	276	832	563	755	225	833	698	739	756	637	848
20-Jul	675	116	491	201	212	138	630	532	434	1,045	157	137	272	373	749	251
21-Jul	908	182	204	450	160	330	667	877	520	1,342	1,247	735	354	168	693	47
22-Jul	1,494	45	333	276	156	474	505	588	691	360	540	400	500	174	364	148
23-Jul	2,803	121	758	402	174	222	40	650	582	436	482	100	450	237	1,212	54
24-Jul	2,744	61	443	71	124	534	547	62	1,244	1,223	123	150	400	84	1,399	152
25-Jul	1,747	124	229	168	300	564	457	666	1,146	1,455	1,154	775	418	260	1,117	594
26-Jul	3,383	178	634	230	678	180	660	691	1,704	1,615	1,452	700	506	428	455	53
27-Jul	1,863	177	438	107	451	312	270	129	1,238	1,055	1,322	25	1,427	158	780	1,534
28-Jul	1,593	277	1,068	242	207	180	40	173	891	3,065	460	47	558	478	1,926	3,026
29-Jul	220	101	1,184	294	230	336	186	725	1,339	1,205	2,021	942	368	65	1,424	307
30-Jul	1,874	675	883	713	291	264	225	349	1,352	3,165	5,215	9	267	387	4,673	39
31-Jul	789	286	2,183	626	185	356	52	986	1,307	4,723	3,417	227	125	245	6,964	39
1-Aug	2,728	358	2,432	38	357	438	113	212	1,616	4,163	2,068	1,268	130	66	5,845	5
2-Aug	2,558	28	970	728	458	162	375	54	1,640	2,207	2,156	1,940	636	858	6,539	130
3-Aug	9,494	332	941	1,314	269	276	420	702	2,579	4,403	171	889	1,015	915	6,670	27
4-Aug	9,175	680	1,724	268	682	180	2,230	1,400	485	1,864	1,286	1,617	191	1,419	2,578	56
5-Aug	8,270	102	1	1,480	1,082	120	1,972	1,415	1,947	2,013	2,143	2,028	78	573	7,338	538
6-Aug	7,858	414	126	834	496	36	983	674	1,285	5,776	690	1,413	56	1,257	9,746	1,919
7-Aug	5,553	281	1,082	795	1,076	240	330	1,832	897	7,054	666	2,465	1,210	2,299	8,135	1,626
8-Aug	7,350	370	1,904	166	1,265	624	15	138	2,695	4,397	761	2,244	348	2,385	7,119	3,245
9-Aug	6,926	569	1,009	516	565	198	4	1,832	2,666	3,581	204	2,183	227	1,531	1,724	7,507
10-Aug	6,574	999	590	1,311	8,270	474	188	128	4,218	4,307	1,718	3,502	40	1,000	4,666	4,291
11-Aug	4,147	699	2,655	1,193	5,569	876	98	1,001	5,373	2,763	6,520	659	120	1,428	907	4,064
12-Aug	7,531	268	2,091	300	6,379	762	113	498	3,812	10,298	4,072	83	1,132	3,836	732	2,495
13-Aug	5,767	421	2,650	238	1,733	570	128	962	1,580	9,469	1,450	4,014	406	2,175	713	6,001

Day	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968
14-Aug	5,823	551	4,001	350	997	534	52	515	2,520	6,516	149	1,019	141	2,691	1,596	3,240
15-Aug	17,049	533	3,970	625	955	354	50	332	1,598	4,985	8,342	1,897	91	6,175	11,476	2,873
16-Aug	6,897	844	2,432	504	325	600	302	1,531	1,853	3,571	11,249	496	61	4,572	27,511	2,357
17-Aug	8,779	970	2,796	171	156	924	7,791	1,307	1,565	2,816	2,170	367	87	3,113	12,173	1,048
18-Aug	16,821	1,093	3,000	816	333	1,158	4,958	1,610	1,207	2,862	711	964	65	2,566	9,397	1,237
19-Aug	12,198	1,249	2,524	488	446	1,008	5,235	1,108	1,909	1,270	1,014	413	147	1,318	9,736	1,253
20-Aug	4,595	1,153	1,595	694	1,403	1,344	15,910	989	2,971	3,756	2,681	366	14,157	1,036	4,237	298
21-Aug	4,277	846	779	435	315	630	4,346	788	686	3,020	8,343	1,003	23,317	2,039	5,219	336
22-Aug	4,780	974	823	335	558	906	930	1,112	9	2,710	8,028	948	8,840	2,214	832	313
23-Aug	6,419	270	449	134	1,129	360	632	1,554	280	5,650	10,141	2,725	2,694	616	1,430	158
24-Aug	2,000	332	192	445	2,976	192	187	1,532	1,891	1,479	42,164	3,622	450	282	1,759	67
25-Aug	7,228	442	72	211	12,503	318	420	3,047	10,318	1,850	18,048	10,192	355	3,438	800	35
26-Aug	10,065	1,347	424	328	10,433	276	627	570	7,916	5,078	6,319	6,054	350	13,828	1,062	224
27-Aug	11,004	1,333	303	210	13,981	306	187	570	1,482	1,409	9,283	3,144	0	22,858	2,652	2,568
28-Aug	3,955	3,006	309	341	3,137	594	9,128	1,329	1,224	32,026	2,543	1,025	0	15,384	5,815	4,612
29-Aug	3,035	8,693	11,360	208	2,893	1,200	6,597	1,073	236	3,308	875	5,500	0	15,145	5,593	8,117
30-Aug	7,694	11,178	21,369	106	1,066	6,384	6,060	1,403	41	1,011	3,424	4,834	0	16,296	5,787	8,476
31-Aug	1,319	4,221	10,530	114	1,816	22,758	4,473	745	0	3,130	7,316	2,695	0	23,151	1,488	6,782
1-Sep	426	7,458	4,375	191	964	9,546	463	1,243	0	4,063	2,157	1,968	5,770	26,507	1,382	3,280
2-Sep	505	10,749	1,637	356	324	2,646	2,280	1,921	0	2,589	4,051	5,289	9,126	20,021	1,312	2,134
3-Sep	350	8,344	17,287	485	650	1,326	40,981	1,791	0	1,025	2,258	6,586	19,125	9,147	3,636	1,894
4-Sep	601	3,699	16,742	650	269	864	21,892	8,550	0	1,984	3,122	11,186	3,032	24,138	3,197	973
5-Sep	2,960	3,863	5,662	1,244	3,724	4,878	5,913	21,721	0	20,930	2,190	3,291	8,568	21,147	2,447	3,668
6-Sep	23,091	4,648	2,615	3,280	1,556	13,188	3,052	15,280	0	22,519	327	15,448	33,325	15,368	445	15,621
7-Sep	43,544	4,018	1,759	3,586	1,482	5,592	2,872	11,127	44	32,401	416	10,159	29,319	14,360	1,052	20,395
8-Sep	15,029	5,898	854	4,967	1,741	444	1,732	5,227	318	23,393	245	15,526	15,176	1,114	1,416	10,126
9-Sep	4,096	6,214	451	2,973	317	54	3,922	1,957	13,217	13,226	1,421	10,337	19,106	4,483	900	3,977
10-Sep	2,164	4,206	767	1,394	462	438	3,142	2,307	9,025	7,162	447	9,010	19,772	11,655	596	8,385
11-Sep	1,349	2,595	2,219	2,094	1,585	294	1,285	2,556	2,587	11,019	1,024	10,525	13,497	11,072	355	4,613
12-Sep	712	3,282	5,444	881	11,152	8,328	1,035	1,534	4,389	9,674	918	6,008	5,467	5,048	1,119	3,221
13-Sep	1,023	2,908	2,851	995	4,482	23,244	5,086	1,131	3,738	1,929	329	500	6,236	4,655	650	1,704
14-Sep	6,222	1,487	11,116	328	5,906	5,814	5,734	3,432	1,148	1,774	412	2,773	10,339	6,078	418	737
15-Sep	5,754	1,598	10,859	12,292	2,030	2,412	6,010	4,376	1,490	789	1,717	1,732	6,074	5,123	482	615
16-Sep	2,460	1,564	8,041	3,758	2,623	1,956	4,633	878	724	368	209	1,047	2,127	5,207	0	302
17-Sep	1,208	5,061	2,085	2,957	561	1,176	1,132	2,746	1,545	3,485	146	912	4,519	3,339	185	105
18-Sep	1,574	7,414	877	1,363	339	354	10,565	43,276	1,958	8,799	2,203	1,077	851	1,791	90	79
19-Sep	10,538	3,866	700	57	128	66	7,115	33,903	830	10,192	1,055	1,235	653	1,161	167	274
20-Sep	16,969	3,362	267	658	391	66	3,267	7,281	1,714	5,481	1,236	8,446	4,516	7,300	1,685	4,176
21-Sep	1,427	1,453	49	488	727	66	5,176	3,065	938	1,282	30	6,647	5,819	3,000	97	6,126
22-Sep	16,609	2,072	54	182	550	60	3,199	1,702	1,789	635	1,129	20,210	246	—	313	2,307
23-Sep	25,166	1,366	176	164	635	60	1,478	1,012	644	644	1,333	18,516	0	—	19	2,135
24-Sep	13,837	221	476	45	554	1,986	1,732	6,277	464	1,209	1,458	11,138	0	—	119	234
25-Sep	7,612	815	12,314	50	773	3,912	12,225	5,018	289	2,651	812	11,700	221	—	126	606
26-Sep	1,775	637	13,250	61	478	252	848	1,856	613	3,722	1,006	10,138	1,129	—	122	3,026
27-Sep	140	316	1,488	430	740	312	2,085	1,153	640	2,353	1,540	5,645	968	—	202	288
28-Sep	1,235	70	583	304	449	42	2,333	409	530	426	8,749	1,784	0	—	350	706
29-Sep	631	59	1,689	265	71	130	3,576	1,139	217	—	1,452	616	962	—	—	1,722
30-Sep	92	34	139	362	241	30	28,115	2,879	329	—	1,212	2,372	0	—	—	1,728

Day	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968
1-Oct	45	—	537	427	30	60	6,715	3,041	401	—	620	1,394	198	—	—	810
2-Oct	13	—	135	1,029	113	—	1,867	3,226	329	—	346	1,662	—	—	—	544
3-Oct	—	—	71	708	0	—	1,005	1,786	—	—	601	1,071	—	—	—	276
4-Oct	—	—	2	409	—	—	585	1,371	—	—	2,592	0	—	—	—	139
5-Oct	—	—	—	152	—	—	283	870	—	—	1,775	548	—	—	—	49
6-Oct	—	—	—	9	—	—	300	914	—	—	533	0	—	—	—	414
7-Oct	—	—	—	—	—	—	315	239	—	—	0	38	—	—	—	—
8-Oct	—	—	—	—	—	—	—	98	—	—	102	163	—	—	—	—
9-Oct	—	—	—	—	—	—	—	151	—	—	210	0	—	—	—	—
10-Oct	—	—	—	—	—	—	—	—	—	—	380	0	—	—	—	—
11-Oct	—	—	—	—	—	—	—	—	—	—	200	0	—	—	—	—
12-Oct	—	—	—	—	—	—	—	—	—	—	406	4	—	—	—	—
13-Oct	—	—	—	—	—	—	—	—	—	—	198	46	—	—	—	—
14-Oct	—	—	—	—	—	—	—	—	—	—	0	33	—	—	—	—
15-Oct	—	—	—	—	—	—	—	—	—	—	192	14	—	—	—	—
16-Oct	—	—	—	—	—	—	—	—	—	—	77	29	—	—	—	—
17-Oct	—	—	—	—	—	—	—	—	—	—	76	—	—	—	—	—
18-Oct	—	—	—	—	—	—	—	—	—	—	107	—	—	—	—	—
19-Oct	—	—	—	—	—	—	—	—	—	—	24	—	—	—	—	—
20-Oct	—	—	—	—	—	—	—	—	—	—	215	—	—	—	—	—
21-Oct	—	—	—	—	—	—	—	—	—	—	85	—	—	—	—	—
22-Oct	—	—	—	—	—	—	—	—	—	—	54	—	—	—	—	—
23-Oct	—	—	—	—	—	—	—	—	—	—	28	—	—	—	—	—
24-Oct	—	—	—	—	—	—	—	—	—	—	0	—	—	—	—	—
25-Oct	—	—	—	—	—	—	—	—	—	—	27	—	—	—	—	—
26-Oct	—	—	—	—	—	—	—	—	—	—	24	—	—	—	—	—
27-Oct	—	—	—	—	—	—	—	—	—	—	18	—	—	—	—	—
28-Oct	—	—	—	—	—	—	—	—	—	—	0	—	—	—	—	—
TOTAL	734,515	326,614	385,719	137,657	220,676	218,814	443,730	347,215	296,636	589,685	405,470	484,077	347,485	455,112	372,464	344,940

Day	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984
10-May	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
11-May	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
12-May	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
13-May	—	—	—	—	—	—	—	—	—	—	0	—	—	—	—	—
14-May	—	—	—	—	—	—	—	—	—	—	0	—	—	—	—	—
15-May	—	—	—	—	—	—	—	—	—	—	0	—	—	—	0	—
16-May	—	—	—	—	—	—	—	—	1	—	0	—	—	—	0	—
17-May	—	—	—	—	—	—	—	—	0	—	0	—	—	—	0	—
18-May	—	—	—	—	—	—	—	—	0	—	1	—	—	—	0	—
19-May	—	—	—	—	—	—	—	—	0	0	1	—	—	—	0	—
20-May	—	—	—	—	—	—	—	—	1	0	3	—	2	0	0	—
21-May	—	—	—	—	—	—	—	—	0	0	2	—	0	3	2	—
22-May	—	—	—	—	—	—	—	—	0	5	1	—	0	2	0	0
23-May	—	—	—	—	—	—	—	0	0	2	0	—	2	0	0	0
24-May	—	—	—	—	—	—	—	0	0	2	0	—	0	0	0	14
25-May	—	—	—	—	—	—	—	0	0	5	2	—	58	0	0	9
26-May	—	—	—	—	—	—	—	5	0	0	0	0	136	1	0	4
27-May	—	0	—	—	—	—	—	0	0	0	1	0	169	2	0	24
28-May	—	5	—	—	—	—	—	2	0	2	18	0	633	0	0	28
29-May	—	16	—	—	—	—	—	9	0	10	143	39	258	11	8	7
30-May	—	12	—	—	—	—	—	48	0	24	78	32	1,196	26	3	79
31-May	0	11	—	0	—	41	—	55	10	30	145	35	454	156	6	8
1-Jun	38	27	—	0	—	31	—	436	0	22	314	25	1,484	127	3	46
2-Jun	6	14	—	1	—	77	—	16	5,518	73	1,268	1,876	1,148	260	258	512
3-Jun	100	37	—	1	—	1,115	16	293	6,617	159	2,252	9,939	963	343	814	11,493
4-Jun	46	11	—	0	—	1,610	36	26	8,067	122	12,567	8,508	3,589	148	10,915	16,408
5-Jun	0	29	—	3	—	216	44	4,207	2,577	367	13,302	7,549	3,504	1,428	14,661	20,161
6-Jun	0	37	—	2	—	3,152	31	2,671	1,328	9,124	6,506	5,136	3,780	1,428	10,534	8,646
7-Jun	0	387	—	0	—	1,533	463	4,873	812	13,222	893	4,688	4,241	1,428	12,416	9,622
8-Jun	3,147	80	—	1	—	150	859	6,003	15,314	10,458	1,045	5,025	7,271	1,429	5,879	3,038
9-Jun	3,147	446	—	20	0	1,268	1,063	498	13,272	3,245	609	6,639	4,600	1,429	3,584	10,542
10-Jun	3,147	1,114	—	35	3,404	2,131	839	4,602	8,497	15,258	1,113	5,867	3,583	1,429	3,449	12,362
11-Jun	3,147	6,833	—	108	3,405	2,570	1,470	6,303	3,340	25,466	12,014	2,953	9,386	1,429	933	11,473
12-Jun	3,147	7,498	—	152	3,404	17,007	1,500	7,138	8,837	5,044	1,869	3,092	6,459	4,647	6,188	9,229
13-Jun	3,147	3,869	0	38	3,405	11,144	2,723	1,807	8,134	9,159	5,832	3,849	6,469	8,856	8,426	5,466
14-Jun	3,147	3,235	0	1,093	3,404	9,656	4,035	11,866	7,052	44,136	16,082	4,471	5,718	7,473	9,578	6,973
15-Jun	3,147	6,832	127	1,585	3,405	6,338	2,272	15,163	4,169	6,483	582	4,165	3,923	5,252	15,199	11,265
16-Jun	3,148	6,435	67	1,024	3,404	3,944	3,711	6,283	2,914	5,725	13,681	5,727	1,965	2,684	11,536	9,885
17-Jun	3,147	7,238	103	2,031	6,746	10,123	1,262	9,123	1,401	7,740	23,316	5,815	3,020	5,651	19,184	10,305
18-Jun	3,147	4,668	70	3,130	6,746	2,870	931	8,273	4,862	10,040	14,493	6,459	2,133	5,521	6,921	7,673
19-Jun	3,147	6,758	74	4,098	6,746	2,385	2,106	14,240	5,268	3,957	16,252	3,848	2,323	3,721	6,596	6,046
20-Jun	3,147	4,512	665	1,554	6,746	3,538	804	3,401	2,165	2,411	7,089	4,347	1,234	1,673	5,642	6,030
21-Jun	3,147	4,994	1,135	5,355	6,746	6,036	1,072	12,608	783	11,345	2,137	2,689	1,472	7,530	6,282	9,184
22-Jun	3,147	3,990	1,530	5,600	6,746	6,116	1,103	12,486	2,486	6,522	4,991	1,283	787	5,988	3,428	6,613
23-Jun	3,147	3,876	617	9,839	6,746	10,016	516	11,254	6,414	4,950	7,196	1,995	930	3,710	3,619	6,572
24-Jun	3,147	3,289	3,453	4,717	3,947	5,035	891	6,311	2,952	2,281	3,131	2,221	1,710	7,830	2,597	3,153
25-Jun	3,147	3,020	4,096	5,663	3,948	6,105	790	4,010	6,000	8,080	2,813	875	2,179	6,014	4,246	3,181
26-Jun	3,147	9,172	6,659	4,046	3,947	6,006	735	5,233	5,692	8,642	3,298	1,244	1,677	2,574	2,623	4,789

Day	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984
27-Jun	3,147	7,612	3,725	4,033	3,948	8,036	1,270	5,134	4,886	6,426	614	2,652	1,904	2,022	4,475	3,812
28-Jun	3,147	2,955	1,234	2,382	3,947	6,360	389	5,102	5,871	2,823	5,617	1,334	1,228	3,758	2,066	5,995
29-Jun	3,147	3,957	20	8,663	3,948	7,497	912	4,746	4,584	2,179	4,204	1,957	1,820	854	3,346	6,063
30-Jun	3,147	923	0	3,810	3,947	7,125	401	4,028	2,678	4,913	1,065	1,250	828	2,200	2,668	5,357
1-Jul	3,147	1,204	0	2,602	2,095	4,511	2,212	4,668	2,309	2,493	10,008	1,920	171	1,400	3,845	6,185
2-Jul	3,147	1,317	0	1,992	2,095	4,901	1,776	2,853	2,932	3,188	1,723	1,850	749	1,801	3,861	3,416
3-Jul	3,148	892	401	2,111	2,095	3,400	2,300	2,282	2,393	2,386	2,342	831	337	2,184	2,672	5,715
4-Jul	3,147	2,240	1,534	4,000	2,094	3,342	0	1,338	695	1,144	1,255	1,090	393	1,558	2,879	3,730
5-Jul	3,147	1,997	2,052	4,761	2,095	1,551	3,029	1,416	2,166	381	1,405	1,097	130	2,527	1,466	8,261
6-Jul	3,147	984	2,451	1,813	2,095	1,032	2,186	3,314	2,863	168	914	1,458	318	2,767	1,755	2,231
7-Jul	3,147	1,010	1,386	4,900	2,095	1,471	1,321	2,018	2,337	1,167	1,012	161	100	2,200	2,128	3,167
8-Jul	3,147	2,113	1,488	3,100	1,420	1,621	1,401	1,039	1,821	1,074	619	329	507	1,506	1,344	4,753
9-Jul	3,147	645	883	1,600	1,419	1,273	895	883	1,548	1,060	2,650	647	40	1,154	474	2,598
10-Jul	3,147	442	782	1,251	1,420	1,315	1,333	697	1,640	1,089	107	598	179	904	457	603
11-Jul	3,147	525	1,103	1,200	1,420	1,516	1,328	168	1,696	1,464	130	55	161	843	552	1,316
12-Jul	216	351	748	1,176	1,420	1,676	781	606	618	197	39	138	93	446	938	1,618
13-Jul	406	369	395	501	1,419	1,019	600	680	1,825	274	563	178	162	374	1,186	1,532
14-Jul	344	466	298	1,205	1,420	212	787	790	1,214	295	301	207	24	1,095	471	1,161
15-Jul	263	316	228	1,220	714	347	429	454	1,725	186	296	292	116	248	173	2,314
16-Jul	49	208	209	455	714	731	309	277	442	1,008	672	302	16	775	557	967
17-Jul	73	221	356	884	714	482	617	227	793	192	600	290	20	520	647	931
18-Jul	163	368	221	509	715	547	324	319	486	69	794	220	30	75	888	1,862
19-Jul	256	252	107	238	714	525	379	267	386	135	286	1,660	53	863	908	712
20-Jul	142	228	286	600	714	91	281	452	1,129	269	494	582	38	363	181	1,111
21-Jul	84	100	228	876	714	17	228	1,036	1,792	50	122	907	64	65	153	2,172
22-Jul	261	54	100	949	468	263	274	826	1,385	44	66	1,519	176	134	522	504
23-Jul	100	213	90	1,007	468	143	127	391	4,248	42	346	1,025	91	367	318	632
24-Jul	424	79	128	1,150	468	253	323	208	7,500	53	482	1,583	30	323	156	642
25-Jul	158	106	198	415	467	164	141	153	3,543	93	180	977	20	283	132	1,040
26-Jul	782	81	99	936	468	289	80	78	4,852	78	197	323	25	453	179	873
27-Jul	1,749	29	104	1,200	468	157	96	94	17,134	159	86	89	9	587	145	327
28-Jul	1,905	136	12	1,689	468	466	99	445	20,007	143	201	93	12	236	522	377
29-Jul	1,100	264	53	835	1,144	408	450	122	6,621	157	91	119	4	293	1,941	261
30-Jul	1,213	266	25	216	1,144	234	568	51	1,971	236	107	23	9	338	1,713	221
31-Jul	1,120	315	0	120	1,144	664	432	283	3,614	2,235	173	14	27	172	820	339
1-Aug	1,444	66	61	183	1,143	427	2,542	498	4,166	602	1,152	11	8	209	4,353	1,282
2-Aug	1,237	46	57	130	1,144	410	1,887	663	1,819	2,536	4,450	1	102	457	4,955	1,296
3-Aug	496	198	60	387	1,144	433	1,310	813	5,711	169	277	54	882	615	2,038	733
4-Aug	321	271	1,476	1,014	1,144	367	1,305	706	2,000	257	75	145	70	605	566	75
5-Aug	1,905	259	1,124	2,150	5,321	632	1,056	1,441	12,709	65	254	331	816	700	4,947	255
6-Aug	2,309	319	1,759	1,227	5,320	503	743	41,506	1,446	62	200	409	1,626	679	1,322	470
7-Aug	364	165	1,303	2,610	5,321	556	1,456	3,878	406	1,906	9,670	118	1,450	421	5,593	402
8-Aug	619	353	2,056	1,076	5,320	380	712	2,027	410	132	4,429	106	30	535	337	59
9-Aug	2,866	161	650	4,049	5,321	708	1,545	9,563	1,958	145	163	66	46	383	90	242
10-Aug	7,344	197	511	3,450	5,320	529	556	502	6,074	3,525	40	44	41	332	72	86
11-Aug	2,157	86	445	1,500	5,321	517	385	303	7,452	2,495	25	16	55	292	92	36
12-Aug	2,158	147	621	1,843	669	1,511	207	326	19,150	10,939	33	256	2,332	151	32	83
13-Aug	1,879	258	223	733	669	1,463	104	201	8,355	5,971	31	27	1,436	307	29	79

Day	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984
14-Aug	2,177	81	100	89	669	815	239	205	211	1,953	36	104	1,583	161	36	88
15-Aug	1,258	146	1,092	115	669	972	37	132	71	3,562	59	947	2,865	66	14	54
16-Aug	294	167	1,103	1,000	669	577	29	146	332	3,762	196	532	118	68	33	307
17-Aug	367	260	1,524	70	669	408	22	71	36,085	1,194	10,640	231	77	60	14,901	916
18-Aug	880	160	594	250	669	186	27	331	8,665	131	5,839	58	113	304	17,022	1,891
19-Aug	7,960	118	855	275	4,025	354	263	264	1,322	207	19,223	298	101	130	370	865
20-Aug	9,351	146	1,747	25	4,026	631	286	114	1,148	4,212	6,029	139	45	204	889	36
21-Aug	4,521	76	941	90	4,025	325	2,525	186	163	530	1,424	122	97	79	381	99
22-Aug	750	73	665	588	4,025	311	20,175	234	135	518	1,454	327	110	353	7,768	86
23-Aug	311	176	99	2,056	4,025	146	19,542	229	327	210	1,434	178	43	298	7,126	47
24-Aug	2,277	37	578	10,145	4,026	272	5,209	550	111	74	4,054	290	109	82	178	100
25-Aug	3,828	57	405	8,313	4,025	231	2,200	10,644	209	31	739	244	29,506	129	74	200
26-Aug	10,937	80	303	1,775	1,211	284	815	15,057	22,975	18	413	170	4,034	261	35	300
27-Aug	15,308	163	100	4,000	1,212	315	2,455	25,197	46,236	105	720	179	3,806	171	11,225	100
28-Aug	12,500	303	274	4,014	1,211	202	5,231	2,095	13,221	191	827	83	1,870	247	4,174	50
29-Aug	8,151	603	89	1,487	1,212	262	5,504	2,336	3,130	571	516	59	1,094	221	615	100
30-Aug	8,936	1,153	118	25	1,211	738	8,678	1,642	2,033	1,570	1,870	105	126	172	4,416	565
31-Aug	8,048	1,821	56	1,000	1,212	1,071	15,356	1,163	3,221	1,210	3,231	929	171	235	770	800
1-Sep	2,076	3,619	107	1,000	1,211	2,506	10,391	400	395	755	13,129	567	86	400	120	300
2-Sep	4,999	6,326	148	129	1,168	10,676	9,516	1,300	136	1,144	4,298	75	78	214	901	300
3-Sep	1,317	7,074	771	1,000	1,167	10,025	2,383	10,648	2,246	548	3,518	24	125	214	279	15,918
4-Sep	1,583	9,538	3,971	150	1,168	10,122	8,067	18,831	1,034	348	5,146	123	7,180	214	21	4,142
5-Sep	1,211	8,326	6,632	0	1,167	12,260	2,226	4,754	1,010	16,625	10,280	120	300	214	35,545	12,500
6-Sep	2,001	7,964	7,424	0	1,168	2,485	13,023	1,068	410	4,818	10,868	145	2,086	214	39,472	10,347
7-Sep	2,359	14,749	415	0	1,167	3,023	18,344	25,493	439	3,348	2,982	17	1,855	215	3,014	13,466
8-Sep	1,786	26,300	3,767	5,009	1,168	2,039	14,524	12,342	4,653	6,906	2,034	709	1,108	215	116	5,576
9-Sep	613	22,310	1,774	7,220	947	2,640	3,621	2,400	658	8,172	298	75	10,328	58	35	4,000
10-Sep	1,664	5,584	778	2,140	946	1,966	5,784	6,486	22,283	3,306	225	28	2,063	134	96	2,000
11-Sep	1,890	3,620	726	4,292	947	1,273	2,833	404	19,653	2,388	345	—	1,950	29	98	1,156
12-Sep	3,442	3,790	191	425	947	1,857	17,115	14	2,581	2,694	1,195	—	98	40	1,788	917
13-Sep	3,550	1,693	252	1,610	947	6,674	16,538	10,580	1,686	2,166	1,498	—	13,216	4,066	4,788	211
14-Sep	7,810	10,266	282	10,000	946	5,725	8,720	303	1,322	2,004	3,834	—	3,629	2,862	3,403	727
15-Sep	4,589	23,084	227	2,000	947	8,636	6,020	35,803	519	1,478	3,308	—	22,257	4,500	113	189
16-Sep	764	16,067	642	1,000	726	2,423	1,689	30,099	1,998	1,122	978	—	766	5,333	58	811
17-Sep	2,853	1,926	7,698	1,625	726	212	4,497	13,134	1,639	75	11,146	—	792	5,333	2,566	699
18-Sep	111	1,276	422	200	726	4,426	3,849	20,000	94	138	3,310	—	111	5,334	18,363	521
19-Sep	1,501	3,142	283	525	727	1,323	27,679	—	536	72	8,627	—	34	—	743	233
20-Sep	2,001	1,481	261	121	726	1,200	13,218	—	152	126	16,754	—	63	—	3,454	76
21-Sep	2,404	794	0	99	726	376	3,013	—	2,434	156	1,404	—	69	—	1,991	56
22-Sep	194	622	5,212	275	726	3,386	5,224	—	1,688	42	20,049	—	1,410	—	1,125	20,789
23-Sep	1,440	176	196	460	192	1,615	2,883	—	1,863	0	5,635	—	—	—	24	11,480
24-Sep	72	116	1,850	225	192	4,184	5,169	—	1,171	0	1,997	—	—	—	11	2,806
25-Sep	500	234	14,297	275	192	4,236	1,403	—	718	0	2,698	—	—	—	1,500	289
26-Sep	244	24	7,229	100	191	3,875	283	—	90	0	12,090	—	—	—	—	169
27-Sep	4,040	43	4,797	24	192	13,358	994	—	7,645	0	1,672	—	—	—	—	150
28-Sep	3,285	623	7,310	29	192	5,335	1,062	—	466	0	1,044	—	—	—	—	100
29-Sep	391	327	811	—	192	0	8,013	—	1	10	170	—	—	—	—	5,000
30-Sep	620	131	1,087	—	433	0	352	—	70	4	16,944	—	—	—	—	—

Day	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984
1-Oct	306	18	549	—	432	0	374	—	27	24	31,208	—	—	—	—	—
2-Oct	1,566	347	211	—	433	0	270	—	52	19	7,790	—	—	—	—	—
3-Oct	1,676	89	407	—	433	0	—	—	30	0	3,145	—	—	—	—	—
4-Oct	100	173	333	—	433	0	—	—	56	4	3,114	—	—	—	—	—
5-Oct	1,433	123	0	—	432	4,567	—	—	4	133	4,000	—	—	—	—	—
6-Oct	5,000	512	313	—	433	0	—	—	57	2	2,100	—	—	—	—	—
7-Oct	948	565	26	—	1,474	0	—	—	0	0	—	—	—	—	—	—
8-Oct	2,553	50	257	—	1,474	0	—	—	0	3	—	—	—	—	—	—
9-Oct	1,665	36	0	—	1,474	0	—	—	—	0	—	—	—	—	—	—
10-Oct	685	7	0	—	1,475	0	—	—	—	166	—	—	—	—	—	—
11-Oct	458	255	62	—	1,474	0	—	—	—	50	—	—	—	—	—	—
12-Oct	—	323	18	—	1,474	7,754	—	—	—	2	—	—	—	—	—	—
13-Oct	—	—	—	—	1,474	—	—	—	—	1	—	—	—	—	—	—
14-Oct	—	—	—	—	—	—	—	—	—	0	—	—	—	—	—	—
15-Oct	—	—	—	—	—	—	—	—	—	0	—	—	—	—	—	—
16-Oct	—	—	—	—	—	—	—	—	—	64	—	—	—	—	—	—
17-Oct	—	—	—	—	—	—	—	—	—	1,062	—	—	—	—	—	—
18-Oct	—	—	—	—	—	—	—	—	—	124	—	—	—	—	—	—
19-Oct	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—
20-Oct	—	—	—	—	—	—	—	—	—	0	—	—	—	—	—	—
21-Oct	—	—	—	—	—	—	—	—	—	0	—	—	—	—	—	—
22-Oct	—	—	—	—	—	—	—	—	—	0	—	—	—	—	—	—
23-Oct	—	—	—	—	—	—	—	—	—	0	—	—	—	—	—	—
24-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
25-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
26-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
27-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
28-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
TOTAL	318,651	313,552	142,265	210,097	252,726	340,565	378,828	523,770	547,254	360,935	513,137	146,623	222,706	164,407	436,145	420,268

Day	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
10-May	—	—	—	—	—	—	—	—	—	0	—	—	—	—	—	—
11-May	—	—	—	—	—	—	—	—	—	0	—	—	—	—	—	—
12-May	—	—	—	—	—	—	—	—	—	0	—	—	—	—	—	—
13-May	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
14-May	—	—	—	—	—	—	—	—	—	0	—	—	—	—	—	—
15-May	—	—	—	—	—	—	—	—	—	0	—	—	—	—	—	—
16-May	—	—	—	—	—	—	—	—	—	0	—	—	—	—	—	—
17-May	—	—	—	—	—	—	—	—	—	0	—	—	—	—	—	—
18-May	—	—	—	—	—	—	—	—	—	9	—	—	—	—	—	—
19-May	—	—	—	—	—	—	—	—	—	0	—	—	3	—	—	—
20-May	—	—	0	—	—	—	—	—	—	1	0	—	3	—	—	—
21-May	—	0	2	—	—	—	—	—	—	0	1	—	2	0	—	—
22-May	—	0	0	—	0	—	—	—	—	2	2	—	4	0	—	—
23-May	0	0	0	—	0	—	—	—	—	4	3	—	6	0	250	—
24-May	0	0	2	—	3	—	—	—	0	0	3	0	8	10	—	—
25-May	0	0	7	0	0	—	—	0	10	0	0	0	26	0	—	0
26-May	6	1	0	53	0	—	0	0	47	1	3	2	41	10	0	64
27-May	2	2	1	397	14	—	10	0	193	6	6	1	146	65	3	57
28-May	128	0	1	41	3	—	1	8	112	4	9	4	175	90	2	38
29-May	138	1	0	117	39	0	6	14	861	6	1	5	71	13	7	9
30-May	60	1	54	135	23	147	0	8	1,721	2	2	3	979	45	17	2
31-May	57	2	64	8	87	176	0	37	7,574	5	4	2	1,313	3,956	768	4
1-Jun	126	21	14	5	18	40	2	202	5,097	5	6	2,434	1,299	3,953	359	9
2-Jun	12	30	3,635	47	1,128	126	3	67	3,982	3	55	5,625	3,662	3,952	275	229
3-Jun	26	9	8,075	304	2,967	89	57	12	8,681	27	32	19,036	154	3,953	76	226
4-Jun	42	39	25,338	544	1,323	325	20	36	10,643	9	68	4,345	300	3,953	1,105	190
5-Jun	75	24	12,476	12,654	10,015	1,140	433	175	12,782	326	182	8,790	1,094	4,000	8,675	538
6-Jun	47	14	14,364	30,000	15,474	5,023	450	741	4,949	93	189	920	4,178	18,118	6,180	77
7-Jun	41	7	18,006	23,000	21,198	7,259	1,240	705	7,232	24	43	147	2,479	14,500	27,901	37
8-Jun	367	208	8,000	7,561	8,303	4,699	216	7,554	18,110	41	42	31	87	15,598	18,878	49,291
9-Jun	24,606	5,325	4,873	4,061	27,053	7,673	340	9,177	22,864	112	1,941	25	143	11,502	27,539	39,376
10-Jun	2,526	11,013	3,065	4,751	33,221	13,010	2,041	9,690	15,558	435	45,804	143	27,943	9,904	29,220	29,122
11-Jun	7,926	13,389	5,552	2,512	19,061	16,206	7,425	6,923	15,001	140	31,981	164	52,839	10,061	11,510	8,109
12-Jun	12,009	28,963	6,438	3,416	4,181	13,518	12,570	4,742	15,626	46,292	15,570	17	12,377	22,086	5,757	7,200
13-Jun	5,834	71,545	6,542	16,191	8,000	14,199	18,890	11,808	22,277	28,627	6,907	8,242	11,365	11,356	22,093	22,203
14-Jun	15,195	18,024	12,603	13,555	1,895	9,815	6,482	12,248	21,498	31,452	393	61,170	17,010	3,178	6,182	3,584
15-Jun	6,391	27,025	7,037	2,702	13,848	7,559	5,107	13,266	19,911	24,451	851	33,557	5,421	8,316	4,664	20,671
16-Jun	3,588	20,354	5,580	8,125	11,993	8,975	6,632	12,703	5,878	17,821	2,389	15,000	7,454	5,802	3,346	20,639
17-Jun	19,251	3,429	34,038	11,758	3,944	5,954	5,388	18,921	5,267	18,289	4,509	161	3,468	8,089	19,695	22,298
18-Jun	15,490	16,624	28,664	10,422	27,765	8,851	11,734	9,776	1,143	16,997	5,384	95	4,054	4,135	32,451	15,594
19-Jun	12,323	7,418	13,476	10,234	15,259	10,005	8,449	10,464	3,689	1,141	7,311	15,326	6,970	4,553	33,352	3,122
20-Jun	18,343	10,858	4,845	18,424	3,595	6,981	6,575	11,571	2,282	6,160	23,661	6,108	7,203	13,111	14,400	5,453
21-Jun	12,301	10,181	19,814	12,521	10,132	2,386	17,011	6,545	1,866	6,140	23,911	23,478	2,382	567	8,957	3,626
22-Jun	13,257	10,907	15,819	10,458	24,392	4,135	12,833	13,121	522	6,651	6,922	2,680	4,165	4,922	21,064	2,155
23-Jun	11,212	6,849	10,754	12,243	3,973	2,340	8,487	12,621	1,893	568	3,469	2,747	7,083	241	12,849	551
24-Jun	14,238	11,619	10,994	7,188	10,535	2,351	7,327	6,341	2,125	1,010	9,541	2,365	10,000	26,319	2,735	2,620
25-Jun	5,110	19,501	7,526	11,682	12,169	2,043	12,210	1,179	1,140	2,839	5,124	979	7,702	9,227	3,450	2,772

Day	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
26-Jun	12,335	19,134	3,681	5,152	9,225	8,282	9,516	5,753	295	832	5,693	1,835	2,181	6,873	4,233	5,143
27-Jun	14,745	10,397	2,880	4,528	11,062	4,657	8,186	5,036	1,062	4,301	1,006	8,118	322	2,341	3,874	331
28-Jun	2,960	5,591	1,442	2,476	8,554	10,282	11,461	3,645	1,271	470	2,920	1,305	697	3,101	11,866	937
29-Jun	6,681	2,755	1,690	2,517	4,021	3,532	8,790	3,173	117	5,848	3,084	349	53	1,169	2,398	349
30-Jun	10,235	4,205	2,662	3,923	2,790	1,703	6,424	1,098	155	3,110	940	2,796	1,313	2,162	2,379	508
1-Jul	5,649	234	2,207	2,756	2,170	2,024	7,900	549	364	2,352	6,250	318	4,437	2,540	4,009	1,544
2-Jul	5,312	456	1,449	5,714	1,131	1,121	6,015	142	2,434	2,180	2,931	1,930	8,147	1,225	3,842	1,332
3-Jul	4,243	55	597	1,691	427	1,377	5,571	331	954	1,133	2,699	2,455	1,316	128	7,201	3,128
4-Jul	5,133	223	1,213	1,160	606	405	2,511	237	1,310	3,669	1,777	3,092	201	172	3,249	2,651
5-Jul	1,808	759	4,290	2,057	1,005	448	5,282	240	540	279	773	740	624	739	821	3,001
6-Jul	13,207	8,063	3,832	3,993	2,374	757	3,893	76	1,094	3,035	342	710	647	551	151	1,992
7-Jul	6,136	8,466	4,713	2,909	1,300	629	2,431	835	1,242	1,517	340	1,209	2,827	91	3,815	3,373
8-Jul	3,662	716	2,891	1,133	489	308	1,093	1,345	1,744	2,989	1,605	3,736	968	713	2,867	1,339
9-Jul	4,261	105	2,755	731	1,642	231	1,666	79	1,802	2,279	175	537	735	691	981	1,644
10-Jul	2,675	80	1,888	1,174	2,714	297	1,677	799	384	1,385	1,588	534	882	734	1,119	197
11-Jul	2,608	318	2,616	742	1,458	502	927	1,600	1,483	1,639	480	518	3,901	973	2,344	224
12-Jul	4,246	3,178	2,185	560	722	164	1,091	1,642	923	332	138	623	2,066	571	659	188
13-Jul	1,322	460	2,463	2,328	289	171	1,043	559	354	2,176	205	258	2,377	1,075	373	505
14-Jul	1,161	56	2,894	1,790	340	141	1,383	1,193	682	3,779	366	1,021	2,621	133	4,423	319
15-Jul	2,978	12	925	1,416	1,391	165	850	524	512	591	435	458	3,695	102	2,608	63
16-Jul	3,068	7	2,844	3,311	1,729	85	861	692	574	282	1,091	1,246	3,616	51	775	884
17-Jul	666	11	1,742	1,131	996	410	284	1,075	372	213	2,176	1,776	819	21	132	185
18-Jul	246	28	3,871	1,858	665	776	710	2,042	416	651	1,100	185	356	121	534	173
19-Jul	432	25	2,832	3,035	242	1,419	222	1,751	161	202	540	266	674	11	1,784	571
20-Jul	63	22	3,494	2,423	85	710	843	1,131	184	116	827	555	24	38	1,549	110
21-Jul	129	17	2,379	893	715	576	547	950	204	5,717	2,279	184	3,754	387	673	794
22-Jul	1,963	2	2,045	992	103	684	667	1,850	408	654	2,851	2,515	1,177	218	343	537
23-Jul	1,961	47	1,475	1,416	336	377	309	532	362	177	678	1,222	93	228	368	275
24-Jul	323	28	315	906	95	445	109	396	32	749	920	22	4,533	428	477	559
25-Jul	305	19	596	1,344	237	409	261	1,035	64	2,324	5,162	1,441	100	57	18	2,403
26-Jul	15	271	335	1,792	284	831	78	960	249	205	797	281	137	103	238	344
27-Jul	4	40	2,300	139	2,027	937	979	1,333	170	1,358	103	22	993	151	893	72
28-Jul	1,722	87	807	87	549	1,703	404	455	100	2,801	95	58	4,680	216	77	346
29-Jul	1,259	65	273	513	1,522	2,088	350	48	285	322	5,317	103	3,997	1,896	1,615	1,148
30-Jul	487	26	1,052	124	570	846	1,440	39	52	95	936	4	1,543	530	151	114
31-Jul	85	26	1,595	786	1,006	629	799	232	478	619	331	192	4,339	1,002	42	1,247
1-Aug	452	109	1,862	3,524	593	2,230	27	149	4,673	410	1,115	168	3,963	670	120	193
2-Aug	92	114	611	242	379	539	648	122	294	88	593	358	1,888	3,051	1,111	4,678
3-Aug	24	141	1,714	15,563	238	2,609	193	214	33	199	5,350	629	2,579	331	79	4,354
4-Aug	108	116	1,575	9,163	5,332	1,705	303	125	89	1,686	341	4,142	899	24	62	4,181
5-Aug	168	288	353	12,056	3,215	1,211	112	146	94	470	89	7,319	940	1,704	17	3,630
6-Aug	4,083	152	646	3,486	2,408	1,186	3,148	314	223	230	342	898	5,118	1,507	221	4,195
7-Aug	695	100	2,331	4,299	1,770	2,028	9,467	1,745	2,263	178	236	704	839	419	178	14,265
8-Aug	418	1,369	8,095	2,355	675	2,455	8,747	4,210	811	507	301	124	1,542	1,533	531	801
9-Aug	312	425	16,887	3,373	3,034	7,807	8,974	1,837	236	733	315	5,482	1,810	1,529	6,851	1,028
10-Aug	162	270	6,466	9,015	10,138	2,880	7,620	2,096	225	1,096	2,807	7,451	174	2,028	458	1,188
11-Aug	638	11	4,705	5,512	20,627	2,538	6,993	1,133	163	1,790	153	7,289	586	787	156	4,898
12-Aug	33,162	685	101	7,188	7,172	12,434	7,562	5,910	97	661	952	10,875	616	815	11,475	1,173

Day	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
13-Aug	21,171	1,777	185	3,589	4,946	9,222	12,068	3,360	63	136	87	344	2,367	1,506	4,952	5,914
14-Aug	13,988	546	1,239	2,433	1,644	3,335	9,291	1,750	365	404	117	560	2,413	1,301	270	2,145
15-Aug	5,788	963	11,738	6,071	368	3,576	7,766	248	151	294	175	295	430	1,163	975	312
16-Aug	2,132	255	22,606	5,779	80	1,378	7,686	1,370	8,347	1,143	641	244	206	5,432	15	402
17-Aug	1,473	1,198	4,766	5,467	64	739	35,595	1,076	328	620	31	775	1,616	6,104	109	1,596
18-Aug	1,275	733	8,167	3,826	471	661	6,033	2,543	1,120	404	662	246	751	1,001	5,641	1,433
19-Aug	984	719	5,197	4,104	136	666	18,220	994	13,641	598	176	784	212	168	12,001	2,310
20-Aug	288	76	356	2,965	218	870	3,616	8,858	2,563	611	80	404	141	732	2,321	1,849
21-Aug	169	252	1,399	3,153	506	4,629	10,546	3,975	297	6,430	132	3,749	545	126	11,971	1,672
22-Aug	319	399	257	1,766	322	3,710	12,633	2,598	56	663	143	6,148	1,677	546	25,987	6,527
23-Aug	650	25	13,612	16,285	17,434	1,265	5,025	26,322	15,678	9,722	9,301	4,200	503	62	14,971	13,133
24-Aug	245	48	1,656	3,519	17,746	428	280	9,564	899	571	7,997	11,926	99	419	3,208	19,645
25-Aug	1,507	10	710	5,573	17,410	394	318	3,858	893	222	3,568	2,485	65	160	797	11,533
26-Aug	16,807	2,547	3,404	5,978	18,218	461	239	38,460	674	146	286	2,426	108	77	145	6,680
27-Aug	27,947	88,766	6,608	547	1,183	3,029	154	14,084	1,596	37	10,424	34	10,182	301	7,040	52,068
28-Aug	3,002	45,020	8,770	589	2,124	892	355	7,284	14,383	85,206	45,478	315	2,220	773	278	13,601
29-Aug	10,908	2,074	7,133	326	2,232	650	179	483	18,373	33,097	6,093	352	3,151	2,241	82	4,476
30-Aug	11,741	79,749	5,138	236	18,011	241	9,923	331	16,943	3,880	21,170	274	477	1,372	65	2,699
31-Aug	14,488	15,270	3,912	181	1,904	21,969	34,521	287	20,160	1,478	2,065	365	33,741	1,118	65	1,733
1-Sep	50,976	9,618	7,561	293	5,332	20,691	22,601	223	1,903	216	2,301	320	23,547	8,489	29	365
2-Sep	37,036	4,901	1,578	232	9,692	46,696	1,250	138	2,488	243	2,213	791	5,302	500	44	161
3-Sep	35,589	3,093	635	328	28,384	87,690	22,621	19,145	818	113	2,484	1,090	1,102	30,000	44,459	87
4-Sep	33,423	9,046	43,973	2,404	53,967	24,431	133,633	9,453	800	113	5,148	925	763	9,716	64,866	81
5-Sep	37,777	11,199	7,086	37,692	89,716	27,113	46,753	62,116	4,868	83	14,518	566	9,093	2,183	26,011	40
6-Sep	22,778	741	28,747	33,058	90,256	1,630	50,915	43,422	2,388	281	13,567	2,192	8,449	1,684	8,253	2,079
7-Sep	13,089	1,500	12,835	22,581	60,406	1,011	18,407	84,060	27,716	100	7,026	69,062	1,175	547	37,248	104
8-Sep	35,464	80,000	217	14,040	10,015	943	2,914	50,165	13,502	150	773	9,330	2,672	530	14,421	3,890
9-Sep	629	30,000	482	177	31,942	225,000	692	15,268	7,704	159	141	4,027	23,530	91	12,585	50
10-Sep	18,804	17,715	7,429	2,500	30,077	—	1,817	332	3,775	749	360	2,041	5,044	226	377	701
11-Sep	10,705	2,441	3,281	2,500	42,910	—	772	393	7,721	1,586	26,791	315	3,323	3,447	14,069	69,278
12-Sep	15,178	479	3,648	2,500	42,877	—	264	44,393	47,578	1,446	18,194	15,000	14,703	1,385	1,778	14,201
13-Sep	47,322	424	81	2,500	28,489	—	42	4,454	20,710	243	6,092	53,000	9,201	5,914	139	19,961
14-Sep	65,917	144	7,135	2,500	14,556	—	161	1,642	12,980	265	388	675	6,891	24,348	228	30,583
15-Sep	7,779	15	226	2,500	7,035	—	148	231	5,063	159,960	9,374	357	8,306	65,051	55	1,271
16-Sep	951	43	50,988	239	5,912	—	53,440	2,453	14,629	65,901	513	5	29,983	21,042	1,188	1,420
17-Sep	285	28	4,368	0	40,000	—	76,831	131	4,206	24,564	7,588	957	7,372	8,131	981	128
18-Sep	6,782	6	4,514	—	—	—	16,052	57	1,200	691	20,381	175	7,932	39,673	156,061	104
19-Sep	22,646	2	9,770	—	—	—	14,373	113	1,688	206	17	2,011	4,628	19,660	37,741	124
20-Sep	15,142	41,097	20,420	—	—	—	63,336	22,931	32,800	56,116	95,108	4,216	3,910	40,445	18,690	95
21-Sep	900	33,012	243	—	—	—	44,489	32,709	4,434	56,097	11,706	7,579	708	11,416	3,957	22,587
22-Sep	7,587	705	10,416	—	—	—	26,821	369	4,068	19,812	6,921	2,013	4,720	964	19,565	52,400
23-Sep	2,620	948	902	—	—	—	35,000	6,222	4,813	26,505	9,377	3,631	11,029	515	10,000	7,826
24-Sep	598	1,325	17,654	—	—	—	20,000	13,122	2,581	8,645	2,586	468	12,720	62	—	6,500
25-Sep	194	2	1,251	—	—	—	3,000	894	2,538	—	25,000	5,998	2,344	45,000	—	—
26-Sep	769	10	2,169	—	—	—	1,000	11,250	6,861	—	78,000	20,000	—	—	—	—
27-Sep	2,000	3,913	863	—	—	—	—	11,250	497	—	—	30,000	—	—	—	10,000
28-Sep	500	15,361	493	—	—	—	—	11,250	20,528	—	—	—	—	—	—	—
29-Sep	500	14,690	200	—	—	—	—	11,250	7,500	—	—	—	—	—	—	—

Day	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
30-Sep	2,000	365	—	—	—	—	—	2,500	—	—	—	—	—	—	—	—
1-Oct	—	387	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2-Oct	—	387	—	—	—	—	—	—	—	—	—	—	—	—	—	—
3-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
4-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
5-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
6-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
7-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
9-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
10-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
11-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
12-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
13-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
14-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
15-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
16-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
17-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
18-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
19-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
20-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
21-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
22-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
23-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
24-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
25-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
26-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
27-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
28-Oct	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
TOTAL	995,948	887,171	766,251	578,816	1,108,646	738,088	1,134,086	831,414	657,455	848,029	743,056	574,325	564,759	637,146	981,538	736,744

Day	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010
10-May	—	—	—	—	—	—	—	—	—	—
11-May	—	—	—	—	—	—	—	—	—	—
12-May	—	—	—	—	—	—	—	—	—	—
13-May	—	—	—	—	—	—	—	—	—	—
14-May	—	—	—	—	—	—	—	—	—	—
15-May	—	—	—	—	—	—	—	—	—	—
16-May	—	—	—	—	—	—	—	—	—	—
17-May	—	—	0	—	—	—	—	—	—	—
18-May	—	—	0	—	—	—	—	—	—	—
19-May	—	—	0	—	—	—	—	—	—	—
20-May	—	—	0	—	—	—	0	—	—	—
21-May	—	—	0	—	—	—	0	—	—	—
22-May	—	—	0	0	—	0	2	—	0	0
23-May	—	0	11	0	—	8	0	0	0	0
24-May	0	4	2	22	—	4	0	0	0	0
25-May	0	5	1	11	—	6	0	0	0	0
26-May	1	6	0	25	—	160	2	0	9	7
27-May	3	5	7	7	0	353	6	0	0	14
28-May	319	152	0	3	445	264	9	0	2	629
29-May	3,588	23	0	7	2	326	4	3	0	35
30-May	3,275	5	2	54	5	3	5	8	2	439
31-May	7,135	24	0	2	6,441	0	3	12	37	39
1-Jun	247	167	199	10	21,412	104	5	3	68	303
2-Jun	16,157	529	0	17	24,409	64	8	0	40	32
3-Jun	11,790	4,787	42,653	17	12,219	230	3	0	126	643
4-Jun	1,487	38,154	40,091	2,720	25,245	89	14	0	256	835
5-Jun	1,693	15,370	90,133	76,308	16,655	57	1	4	123	290
6-Jun	20,625	22,997	28,587	75,810	4,294	23	0	0	41	1,229
7-Jun	12,659	22,879	23,644	37,418	36	11	3	6	4,592	795
8-Jun	19,538	12,754	37,312	37,477	290	0	1	97	43	45
9-Jun	47,775	11,358	15,775	2,412	2	7,087	4,148	4	1,603	123
10-Jun	39,512	19,946	18,696	2,351	603	18,601	20,883	0	859	58
11-Jun	37,082	24,576	1,534	30,154	1	30,381	24,916	1	2,981	61
12-Jun	27,455	29,023	13,091	36,422	563	15,373	4,621	1	3,575	50
13-Jun	25,966	38,298	15,049	12,475	4,260	9,587	17,656	0	3,064	451
14-Jun	16,853	25,769	11,641	3,094	31,690	128	46,784	6	2,052	42
15-Jun	10,959	35,104	7,450	324	10,758	32	21,336	49	3,096	162
16-Jun	9,663	23,994	9	20,609	10,500	216	37,628	26	89	30
17-Jun	2,580	19,849	12	7,803	698	277	162	39	136	275
18-Jun	2,380	11,380	1,005	2,821	4,127	24	45	16,291	84	249
19-Jun	1,998	8,576	22,180	10,751	2,064	82	19,701	31,567	50	9,471
20-Jun	1,637	13,380	1,920	4,714	541	15,551	7,899	10,681	4,123	25,069
21-Jun	4,357	7,048	5,520	3,352	10,551	28,534	26,077	3,885	11,164	8,092
22-Jun	2,157	8,076	6,860	508	8,592	2,730	5,888	0	1,022	1,027
23-Jun	812	5,792	411	682	15,277	9,120	41	497	17	370
24-Jun	580	5,041	448	121	1,098	33	489	7	1,961	292
25-Jun	672	2,061	15,277	562	4,217	6	44	5	970	2,857
26-Jun	89	1,206	7,884	776	5,525	11	77	3	1,741	429
27-Jun	382	1,357	1,418	87	1,901	9,942	4,230	646	258	1,012
28-Jun	106	12,176	1,693	113	2,576	9,544	143	1	1,273	313
29-Jun	131	1,235	6,976	1,505	3,153	2,184	5,651	3,503	632	539
30-Jun	387	5,114	2,259	74	753	2	58	7,351	79	1,930
1-Jul	136	6,768	821	4,069	1,032	16,275	1,749	1,563	2,060	329
2-Jul	151	1,271	887	1,116	6,130	2,449	13,748	155	1,712	5,003
3-Jul	375	266	1,830	157	3,202	4,534	5,757	5,011	33	1,773
4-Jul	89	2,133	6,013	79	2,010	437	49	203	5	381
5-Jul	302	1,532	2,697	2,628	125	1,667	26	91	106	1,066
6-Jul	139	2,260	1,123	668	8,997	1,171	4	230	831	267
7-Jul	253	1,983	522	158	570	2,032	1	59	1,121	531
8-Jul	125	2,751	1,421	986	3,982	385	1	24	130	327
9-Jul	108	1,540	852	717	521	275	3	20	6	37
10-Jul	224	2,127	1,136	242	3,367	1,587	0	7	8	937
11-Jul	227	489	1,875	137	1,321	5,615	17	0	104	28
12-Jul	462	967	7,630	687	1,973	1,696	127	7	158	107
13-Jul	488	39	160	3,727	1,416	429	9,357	2	3	1,324
14-Jul	1,127	1,035	502	512	1,390	9	7	1	11	33
15-Jul	842	114	782	1,540	1,362	933	1	2	10	164

Day	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010
16-Jul	128	527	1,581	946	2,579	1,604	53	4	228	77
17-Jul	15	1,117	327	35	639	0	9,065	15	4	505
18-Jul	111	477	31	196	1,541	2	50	1	0	81
19-Jul	700	575	246	815	5,442	1	15	24	3	144
20-Jul	496	417	761	842	2,446	18	5,251	29	97	81
21-Jul	249	234	909	1,593	2,912	100	916	47	0	21
22-Jul	120	303	171	1,364	163	32	1,653	0	5	23
23-Jul	255	136	589	216	1,467	48	1,695	23	3	1
24-Jul	220	938	17	232	502	7,301	18	186	5	26
25-Jul	74	378	74	127	308	778	3,270	17,272	1	58
26-Jul	67	375	109	965	1,749	12	6,672	2,061	16	222
27-Jul	174	206	581	35	646	47	213	130	152	24
28-Jul	110	361	378	10	221	1,067	131	195	107	47
29-Jul	297	609	96	2	797	65	16	89	68	351
30-Jul	873	8,087	61	8	1,643	40	495	77	2	460
31-Jul	2,477	3,809	7,092	871	523	92	3,195	487	713	637
1-Aug	20,096	1,857	1,780	6	6,447	536	1	433	28	358
2-Aug	14,080	1,943	3,412	22	437	6,264	97	1,116	187	25
3-Aug	12,249	650	336	5,293	4,000	112	56	65	25	233
4-Aug	752	141	225	80	390	6,896	392	63	584	129
5-Aug	21,961	1,886	199	371	99	74	1,836	70	546	964
6-Aug	7,737	389	4,377	118	29	13	53	1,569	24	192
7-Aug	3,192	189	179	556	531	3	13	679	140	305
8-Aug	4,401	804	54	6,233	110	109	614	834	14	158
9-Aug	8,658	473	730	4,698	456	937	100	241	50	2,221
10-Aug	2,752	4,955	259	2,174	671	35	184	119	146	398
11-Aug	4,401	2,102	3,353	2,729	17	663	64	2	109	1,789
12-Aug	2,417	779	16,747	2,531	664	334	35	54	45	494
13-Aug	8,467	407	5,867	315	478	151	25	157	111	51
14-Aug	19,284	1,228	37,759	237	527	63	495	137	10	78
15-Aug	8,291	5,903	8,946	201	484	646	140	334	239	345
16-Aug	11,013	5,766	7,273	626	504	978	62	133	11	203
17-Aug	39,927	559	12,243	1,274	9,411	11,172	210	192	18	191
18-Aug	15,982	252	2,879	899	3,778	3,479	48	39	18	54
19-Aug	885	81	481	901	3,565	8,234	66	89	39	585
20-Aug	34,302	469	25,892	44	306	5,978	56	844	41	3,635
21-Aug	5,546	275	17,296	400	1,993	775	25	510	40	2,343
22-Aug	19,604	222	1,761	332	189	2,444	26	290	18	1,295
23-Aug	653	77	2,213	641	13,801	299	176	114	1,264	1,636
24-Aug	635	152	814	10,552	3,249	195	7,936	85	68	782
25-Aug	891	657	295	2,464	231	1,732	332	42	171	2,552
26-Aug	1,429	183	15,894	1,206	2,406	1,047	13	34	58	3,907
27-Aug	1,133	248	11,793	3,811	10,082	2,393	45	1,627	94	5,217
28-Aug	13,531	556	26,044	1,440	3,632	3,873	94	4,384	33	1,644
29-Aug	22,199	993	17,350	833	255	3,705	8,940	2,069	10,942	753
30-Aug	22,708	34,135	7,746	551	48,253	551	6,949	282	1,191	601
31-Aug	50,008	13,915	12,276	540	4,926	9,245	603	23	533	1,662
1-Sep	19,826	4,866	29,647	2,428	4,749	3,124	72	7,233	195	1,221
2-Sep	21,802	5,177	1,005	4,308	1,938	87	119	295	210	1,295
3-Sep	1,069	2,118	35,345	4,264	178	2,345	61	5,281	424	499
4-Sep	565	20,735	6,171	4,720	716	3,360	146	179	6,477	491
5-Sep	671	58,633	1,338	10,798	125	2,065	26,372	207	18,023	69,158
6-Sep	652	24,096	51,016	9,827	13,668	5,791	3,145	57	13,569	20,885
7-Sep	7,010	16,834	16,558	6,834	25,911	1,964	576	27	433	54,669
8-Sep	8,040	10,571	1,797	560	1,043	30,134	17,285	150	154	249
9-Sep	3,201	4,614	18,373	36,758	14,715	9,144	5,086	40,000	782	569
10-Sep	710	960	20,181	13,836	55,277	5,807	345	10,169	67	343
11-Sep	2,287	364	11,982	28,845	8,086	5,255	16	174	153	286
12-Sep	1,595	240	13,223	3,772	3,641	5,268	234	236	115	94
13-Sep	2,537	273	1,075	9,780	8,845	804	21	67	69	24
14-Sep	3,811	96	4,515	4,735	15,336	50,048	13,909	144	353	20
15-Sep	384	91	21,831	20,519	20,831	15,246	1,054	290	2,413	44
16-Sep	336	181	5,575	5,308	36,618	4,116	175	412	296	21
17-Sep	46,792	20,633	8,715	4,344	291	5,106	48,141	23	30,495	67
18-Sep	5,600	30,242	579	2,992	31,491	837	512	158	25,042	65
19-Sep	14,000	18,655	4,329	5,085	3,384	15,088	27,936	23,809	1,373	90,000
20-Sep	—	606	57	12,628	17,181	—	533	2,175	22	—

Day	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010
21-Sep	—	302	872	8,322	317	—	1,931	6,063	75	—
22-Sep	—	1,803	1,931	14,884	2,685	—	300	30,000	358	—
23-Sep	—	63,825	0	774	21,136	—	24,068	—	29	—
24-Sep	—	7,000	20,553	1,704	80,000	—	10,593	—	12	—
25-Sep	—	2,767	39,991	10,166	—	—	2,161	—	29	—
26-Sep	—	2,586	19,354	5,661	—	—	20,000	—	2,089	—
27-Sep	—	1,018	200	9,887	—	—	—	—	77,489	—
28-Sep	—	12,000	35,000	20,136	—	—	—	—	13,664	—
29-Sep	—	—	—	5,310	—	—	—	—	65,000	—
30-Sep	—	—	—	200	—	—	—	—	—	—
1-Oct	—	—	—	200	—	—	—	—	—	—
2-Oct	—	—	—	742	—	—	—	—	—	—
3-Oct	—	—	—	0	—	—	—	—	—	—
4-Oct	—	—	—	200	—	—	—	—	—	—
5-Oct	—	—	—	300	—	—	—	—	—	—
6-Oct	—	—	—	—	—	—	—	—	—	—
7-Oct	—	—	—	—	—	—	—	—	—	—
8-Oct	—	—	—	—	—	—	—	—	—	—
9-Oct	—	—	—	—	—	—	—	—	—	—
10-Oct	—	—	—	—	—	—	—	—	—	—
11-Oct	—	—	—	—	—	—	—	—	—	—
12-Oct	—	—	—	—	—	—	—	—	—	—
13-Oct	—	—	—	—	—	—	—	—	—	—
14-Oct	—	—	—	—	—	—	—	—	—	—
15-Oct	—	—	—	—	—	—	—	—	—	—
16-Oct	—	—	—	—	—	—	—	—	—	—
17-Oct	—	—	—	—	—	—	—	—	—	—
18-Oct	—	—	—	—	—	—	—	—	—	—
19-Oct	—	—	—	—	—	—	—	—	—	—
20-Oct	—	—	—	—	—	—	—	—	—	—
21-Oct	—	—	—	—	—	—	—	—	—	—
22-Oct	—	—	—	—	—	—	—	—	—	—
23-Oct	—	—	—	—	—	—	—	—	—	—
24-Oct	—	—	—	—	—	—	—	—	—	—
25-Oct	—	—	—	—	—	—	—	—	—	—
26-Oct	—	—	—	—	—	—	—	—	—	—
27-Oct	—	—	—	—	—	—	—	—	—	—
28-Oct	—	—	—	—	—	—	—	—	—	—
TOTAL	863,536	865,576	1,078,710	720,203	781,962	450,373	546,575	246,490	330,077	348,102

— = weir not in operation; 0 = weir in operation, but no fish counted. Weir starting and ending dates are unclear in some years. Some escapements in September–October are estimates (often rounded to the nearest 1,000 or 10,000), not counts, of sockeye salmon holding in Karluk Lagoon downstream of the weir when the weir-counting season ended.

APPENDIX 6

Summary of Scales Collected from Karluk's Sockeye Salmon

Sockeye salmon scales provide valuable data on age compositions and growth conditions of sampled populations. The collection information has immediate interest, but it also has long-term value as records of past populations and environmental conditions that can be reexamined and reinterpreted when biological questions arise. In addition, future advancements in fisheries research and technologies may extract new information from previously collected scales. Thus, scale collections have value beyond their original purpose and should be organized and preserved at a known location or archival facility.

Sockeye salmon scales have been collected annually at Karluk since the 1920s, and a few samples date back to 1914. Typically, 2,000-4,000 adult fish were sampled each year, but sometimes the number approached 10,000. Less regularly, numerous juvenile and smolt scales were sampled. Federal (USBF, FWS, BCF) and state (ADF, ADFG) agencies collected most sockeye salmon scales, but during 1948–58, the Fisheries Research Institute, University of Washington, sampled thousands of Karluk's sockeye salmon.

The following table summarizes the sockeye salmon scale collections at Karluk. Two sources supplied most of the table's data: 1) a 1998 inventory by ADFG biologist Patricia A. Nelson of scales and scale impressions located at ADFG Kodiak, NARA, FRI, and ABL, and 2) a 1996 list by ABL biologist Herbert W. Jaenicke of scales and scale impressions stored at NARA, Anchorage.

In addition to sockeye salmon scales collected by fishery biologists since 1914, fish scales, vertebrae, and other parts have been unearthed in archaeological excavations at Karluk and archived at the Alutiiq Museum, Kodiak. These prehistoric materials may have value for understanding past environments and sockeye salmon populations at Karluk.

Year	Storage location	Number collected
1914	Unknown	Some?
1915	Unknown	None?
1916	Unknown	382
1917	Unknown	758
1918	Unknown	None?
1919	Unknown	103
1920	Unknown	None?
1921	Unknown	211
1922	Unknown	2469
1923	Unknown	None?
1924	NARA ABL	5132
1925	NARA ABL	5513
1926	NARA ABL	8172
1927	NARA ABL	4963
1928	NARA ABL	4247
1929	NARA ABL	1602
1930	NARA ABL	3617
1931	NARA ABL	7258
1932	NARA ABL	4700
1933	NARA ABL	3867
1934	NARA ABL	6551
1935	NARA ABL	7152
1936	NARA ABL	7093
1937	NARA ABL	
1938	NARA ABL	
1939	NARA ABL	
1940	NARA ABL	7700
1941	NARA ABL	2700
1942	NARA ABL	
1943	NARA ABL	
1944	NARA ABL	7350
1945	Unknown	
1946	NARA ABL	
1947	NARA ABL	

Year	Storage location	Number collected
1948	NARA ABL FRI	
1949	NARA ABL FRI	
1950	NARA ABL FRI	
1951	NARA ABL FRI	
1952	NARA FRI	
1953	NARA FRI	
1954	NARA FRI	
1955	NARA FRI	
1956	NARA FRI	3236
1957	NARA FRI	
1958	NARA ABL FRI	
1959	NARA	
1960	NARA	
1961	NARA	
1962	NARA	2237
1963	NARA	2022
1964	NARA	2410
1965	NARA	1712
1966	NARA	2233
1967	NARA	1758
1968	NARA	1702
1969	NARA	
1970	ADFG Kodiak	1054
1971	ADFG Kodiak	471
1972	ADFG Kodiak	
1973	ADFG Kodiak	
1974	ADFG Kodiak	
1975	ADFG Kodiak	
1976	ADFG Kodiak	
1977	ADFG Kodiak	none early
1978	ADFG Kodiak	
1979	ADFG Kodiak	none early
1980	ADFG Kodiak	
1981	ADFG Kodiak	

Year	Storage location	Number collected
1982	ADFG Kodiak	
1983	ADFG Kodiak	
1984	ADFG Kodiak	
1985	ADFG Kodiak	2336
1986	ADFG Kodiak	1383
1987	ADFG Kodiak	3086
1988	ADFG Kodiak	2446
1989	ADFG Kodiak	2728
1990	ADFG Kodiak	2960
1991	ADFG Kodiak	2948
1992	ADFG Kodiak	2746
1993	ADFG Kodiak	3252
1994	ADFG Kodiak	2973
1995	ADFG Kodiak	2545
1996	ADFG Kodiak	
1997	ADFG Kodiak	
1998	ADFG Kodiak	
1999	ADFG Kodiak	
2000	ADFG Kodiak	
2001	ADFG Kodiak	
2002	ADFG Kodiak	
2003	ADFG Kodiak	
2004	ADFG Kodiak	
2005	ADFG Kodiak	
2006	ADFG Kodiak	
2007	ADFG Kodiak	
2008	ADFG Kodiak	
2009	ADFG Kodiak	
2010	ADFG Kodiak	

ABL = Auke Bay Laboratory, Auke Bay, AK
ADFG = Alaska Department of Fish and Game, Kodiak, AK
FRI = Fisheries Research Institute, University of Washington, Seattle, WA
NARA = National Archives and Records Administration, Anchorage, AK

APPENDIX 7

Karluk River Sockeye Salmon Ages and Life Cycles

Age 2-3

Age	Year	Life cycle[1] (Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec)	FW-SW[2] Scale Annuli
$2_1 = 0.1$	0	Eggs in gravel o o o o o o o o o o	0
	1	o o o o o o o o o Fry to lake - Smolts to sea s s s s s s s s s s s s s s	1
	2	s s s s s s s s s s s s Adults return to spawn & die	
$3_1 = 0.2$	0	Eggs in gravel o o o o o o o o o o	0
	1	o o o o o o o o o Fry to lake - Smolts to sea s s s s s s s s s s s s s s	2 (years 1–2)
	2	s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s	
	3	s s s s s s s s s s s s Adults return to spawn & die	
$3_2 = 1.1$	0	Eggs in gravel o o o o o o o o o o	
	1	o o o o o o o o o Fry to lake f f f f f f f f f f f f f f f f f f f f f	1
	2	f f f f f f f f f f f f f f Smolts to sea s s s s s s s s s s s s s s	1
	3	s s s s s s s s s s s s Adults return to spawn & die	
$3_3 = 2.0$	0	Eggs in gravel o o o o o o o o o o	
	1	o o o o o o o o o Fry to lake f f f f f f f f f f f f f f f f f f f f f	2 (years 1–2)
	2	f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f	
	3	f f f f f f f f f f f f f Smolts to sea - Adults return to spawn & die	0

[1] o = Eggs and aelvins incubating in substrate; f = juvenile growth in freshwater; s = growth in the ocean

[2] FW = Freshwater; SW = Saltwater

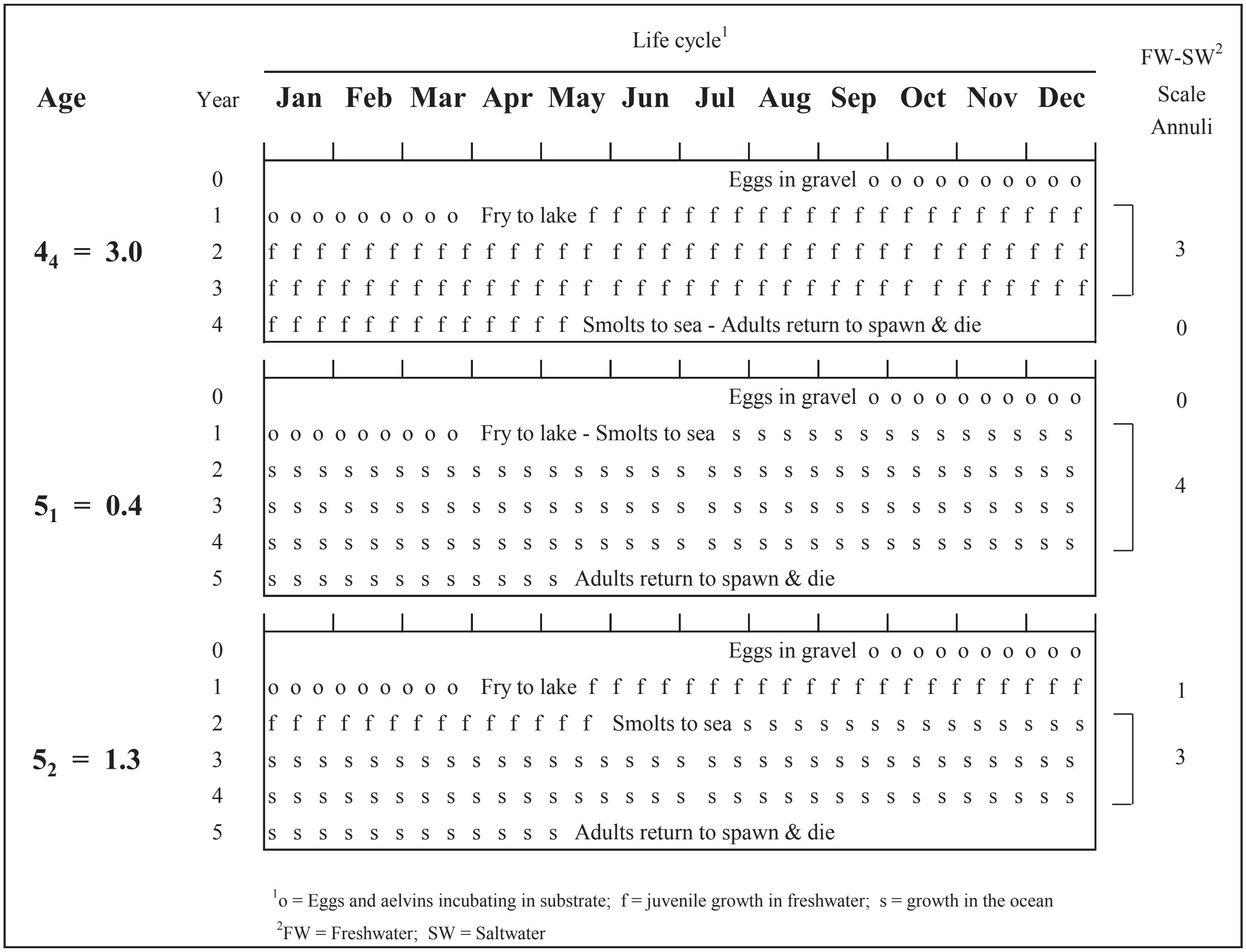
Age 4

Age	Year	Life cycle[1] (Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec)	FW-SW[2] Scale Annuli
	0	Eggs in gravel o o o o o o o o o o	0
	1	o o o o o o o o o Fry to lake - Smolts to sea s s s s s s s s s s s s s s	
$4_1 = 0.3$	2	s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s	3
	3	s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s	
	4	s s s s s s s s s s s s Adults return to spawn & die	
	0	Eggs in gravel o o o o o o o o o o	
	1	o o o o o o o o o Fry to lake f f f f f f f f f f f f f f f f f f f f f	1
$4_2 = 1.2$	2	f f f f f f f f f f f f f f Smolts to sea s s s s s s s s s s s s s s	2
	3	s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s	
	4	s s s s s s s s s s s s Adults return to spawn & die	
	0	Eggs in gravel o o o o o o o o o o	
	1	o o o o o o o o o Fry to lake f f f f f f f f f f f f f f f f f f f f f	2
$4_3 = 2.1$	2	f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f	
	3	f f f f f f f f f f f f f f Smolts to sea s s s s s s s s s s s s s s	1
	4	s s s s s s s s s s s s Adults return to spawn & die	

[1] o = Eggs and aelvins incubating in substrate; f = juvenile growth in freshwater; s = growth in the ocean

[2] FW = Freshwater; SW = Saltwater

Age 4-5



Life cycle[1]
Age
Year
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
FW-SW[2] Scale Annuli
4_4 = 3.0
0 Eggs in gravel o o o o o o o o o o
1 o o o o o o o o o Fry to lake f f f f f f f f f f f f f f f f f f f f f
2 f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f
3 f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f
4 f f f f f f f f f f f f f Smolts to sea - Adults return to spawn & die
3
0
5_1 = 0.4
0 Eggs in gravel o o o o o o o o o o
1 o o o o o o o o o Fry to lake - Smolts to sea s s s s s s s s s s s s s s
2 s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s
3 s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s
4 s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s
5 s s s s s s s s s s s s Adults return to spawn & die
0
4
5_2 = 1.3
0 Eggs in gravel o o o o o o o o o o
1 o o o o o o o o o Fry to lake f f f f f f f f f f f f f f f f f f f f f
2 f f f f f f f f f f f f f f Smolts to sea s s s s s s s s s s s s s s
3 s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s
4 s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s
5 s s s s s s s s s s s s Adults return to spawn & die
1
3
[1]o = Eggs and aelvins incubating in substrate; f = juvenile growth in freshwater; s = growth in the ocean
[2]FW = Freshwater; SW = Saltwater

Age 5

Age	Year	Life cycle[1] (Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec)	FW-SW[2] Scale Annuli
5_3 = 2.2	0	Eggs in gravel o o o o o o o o o o	
	1	o o o o o o o o o Fry to lake f f f f f f f f f f f f f f f f f f f f f	
	2	f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f	2
	3	f f f f f f f f f f f f f f Smolts to sea s s s s s s s s s s s s s s	
	4	s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s	2
	5	s s s s s s s s s s s s Adults return to spawn & die	
5_4 = 3.1	0	Eggs in gravel o o o o o o o o o o	
	1	o o o o o o o o o Fry to lake f f f f f f f f f f f f f f f f f f f f f	
	2	f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f	3
	3	f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f	
	4	f f f f f f f f f f f f f f Smolts to sea s s s s s s s s s s s s s s	1
	5	s s s s s s s s s s s s Adults return to spawn & die	
5_5 = 4.0	0	Eggs in gravel o o o o o o o o o o	
	1	o o o o o o o o o Fry to lake f f f f f f f f f f f f f f f f f f f f f	
	2	f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f	
	3	f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f	4
	4	f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f	
	5	f f f f f f f f f f f f f Smolts to sea - Adults return to spawn & die	0

[1] o = Eggs and aelvins incubating in substrate; f = juvenile growth in freshwater; s = growth in the ocean

[2] FW = Freshwater; SW = Saltwater

Age 6

Age	Year	Life cycle[1] Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec	FW-SW[2] Scale Annuli
	0	Eggs in gravel o o o o o o o o o o	
	1	o o o o o o o o o Fry to lake f f f f f f f f f f f f f f f f f f f f f	1
	2	f f f f f f f f f f f f f f Smolts to sea s s s s s s s s s s s s s s	
6_2 = 1.4	3	s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s	4
	4	s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s	
	5	s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s	
	6	s s s s s s s s s s s s Adults return to spawn & die	
	0	Eggs in gravel o o o o o o o o o o o	
	1	o o o o o o o o o Fry to lake f f f f f f f f f f f f f f f f f f f f f	2
	2	f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f	
6_3 = 2.3	3	f f f f f f f f f f f f f f Smolts to sea s s s s s s s s s s s s s s	
	4	s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s	3
	5	s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s	
	6	s s s s s s s s s s s s Adults return to spawn & die	
	0	Eggs in gravel o o o o o o o o	
	1	o o o o o o o o o Fry to lake f f f f f f f f f f f f f f f f f f f f f	
	2	f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f	3
6_4 = 3.2	3	f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f	
	4	f f f f f f f f f f f f f f Smolts to sea s s s s s s s s s s s s s s	2
	5	s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s	
	6	s s s s s s s s s s s s s s s s s Adults return to spawn & die	

[1]o = Eggs and aelvins incubating in substrate; f = juvenile growth in freshwater; s = growth in the ocean

[2]FW = Freshwater; SW = Saltwater

Age 6-7

Age	Year	Life cycle[1] (Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec)	FW-SW[2] Scale Annuli
6_5 = 4.1	0	Eggs in gravel o o o o o o o o o o	
	1	o o o o o o o o o Fry to lake f f f f f f f f f f f f f f f f f f f f f	4 (years 1–4)
	2	f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f	
	3	f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f	
	4	f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f	
	5	f f f f f f f f f f f f f f Smolts to sea s s s s s s s s s s s s s s s	1
	6	s s s s s s s s s s s s Adults return to spawn & die	
7_3 = 2.4	0	Eggs in gravel o o o o o o o o o o	
	1	o o o o o o o o o Fry to lake f f f f f f f f f f f f f f f f f f f f f	2 (years 1–2)
	2	f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f	
	3	f f f f f f f f f f f f f f Smolts to sea s s s s s s s s s s s s s s s	4 (years 3–6)
	4	s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s	
	5	s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s	
	6	s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s	
	7	s s s s s s s s s s s s Adults return to spawn & die	
7_4 = 3.3	0	Eggs in gravel o o o o o o o o o o	
	1	o o o o o o o o o Fry to lake f f f f f f f f f f f f f f f f f f f f f	3 (years 1–3)
	2	f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f	
	3	f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f	
	4	f f f f f f f f f f f f f f Smolts to sea s s s s s s s s s s s s s s s	3 (years 4–6)
	5	s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s	
	6	s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s	
	7	s s s s s s s s s s s s Adults return to spawn & die	

[1]o = Eggs and aelvins incubating in substrate; f = juvenile growth in freshwater; s = growth in the ocean

[2]FW = Freshwater; SW = Saltwater

Age 7-8

Age	Year	Life cycle[1] (Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec)	FW-SW[2] Scale Annuli
$7_5 = 4.2$	0	Eggs in gravel o o o o o o o o o o	
	1	o o o o o o o o o Fry to lake f f f f f f f f f f f f f f f f f f f f f	4 (years 1–4)
	2	f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f	
	3	f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f	
	4	f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f	
	5	f f f f f f f f f f f f f f Smolts to sea s s s s s s s s s s s s s s	2 (years 5–6)
	6	s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s	
	7	s s s s s s s s s s s s Adults return to spawn & die	

Age	Year	Life cycle[1] (Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec)	FW-SW[2] Scale Annuli
$8_3 = 2.5$	0	Eggs in gravel o o o o o o o o o o	
	1	o o o o o o o o o Fry to lake f f f f f f f f f f f f f f f f f f f f f	2 (years 1–2)
	2	f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f	
	3	f f f f f f f f f f f f f f Smolts to sea s s s s s s s s s s s s s s	5 (years 3–7)
	4	s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s	
	5	s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s	
	6	s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s	
	7	s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s	
	8	s s s s s s s s s s s s Adults return to spawn & die	

[1] o = Eggs and aelvins incubating in substrate; f = juvenile growth in freshwater; s = growth in the ocean

[2] FW = Freshwater; SW = Saltwater

Age 8

Age	Year	Life cycle[1]: Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec	FW-SW[2] Scale Annuli
	0	Eggs in gravel o o o o o o o o o o	
	1	o o o o o o o o o Fry to lake f f f f f f f f f f f f f f f f f f f f f	3
	2	f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f	
	3	f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f	
8_4 = 3.4	4	f f f f f f f f f f f f f f Smolts to sea s s s s s s s s s s s s s s	4
	5	s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s	
	6	s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s	
	7	s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s	
	8	s s s s s s s s s s s s Adults return to spawn & die	

Age	Year	Life cycle[1]: Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec	FW-SW[2] Scale Annuli
	0	Eggs in gravel o o o o o o o o o o	
	1	o o o o o o o o o Fry to lake f f f f f f f f f f f f f f f f f f f f f	4
	2	f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f	
	3	f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f	
8_5 = 4.3	4	f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f	
	5	f f f f f f f f f f f f f f Smolts to sea s s s s s s s s s s s s s s	3
	6	s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s	
	7	s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s	
	8	s s s s s s s s s s s s Adults return to spawn & die	

[1]o = Eggs and aelvins incubating in substrate; f = juvenile growth in freshwater; s = growth in the ocean

[2]FW = Freshwater; SW = Saltwater

Age 9

Age	Year	Life cycle[1] (Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec)	FW-SW[2] Scale Annuli
	0	Eggs in gravel o o o o o o o o o o	
	1	o o o o o o o o o Fry to lake f f f f f f f f f f f f f f f f f f f f f	4
	2	f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f	
	3	f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f	
	4	f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f f	
9_5 = 4.4	5	f f f f f f f f f f f f f f Smolts to sea s s s s s s s s s s s s s s	4
	6	s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s	
	7	s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s	
	8	s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s s	
	9	s s s s s s s s s s s s Adults return to spawn & die	

[1]o = Eggs and aelvins incubating in substrate; f = juvenile growth in freshwater; s = growth in the ocean

[2]FW = Freshwater; SW = Saltwater

Karluk Biological Resources

During our search for information on Karluk's sockeye salmon and associated biota, we incidentally learned about reference specimens held in various museums. Since these preserved and archived collections are valuable Karluk resources, their locations are listed below. The following summary is not an exhaustive list of Karluk specimens held in museums or institutions worldwide, but it does show where at least some collections exist.

Algae

1899: University of California Expedition—Marine algae from Karluk, Uyak, and Kodiak are present in the Herbarium of the University of California, Berkeley. These were collected in the summer of 1899, primarily by William Albert Setchell and A. A. Lawson, but also by W. L. Jepson and L. E. Hunt. A summary of Karluk's marine algae was published by Setchell and Gardner (1903).

1926–27: Willis H. Rich (1885–1972)—Diatoms from Karluk, Thumb, and O'Malley lakes are present at the US National Museum, Washington, DC. These diatoms were originally collected by Rich and then became part of the Albert Mann and Paul S. Conger collections before being deposited in the US National Museum.

1940s: A. L. Brigger—Diatoms collected from stones at Camp Island and the Karluk River, and from boards at the Karluk River weir, are located in the Diatom Collection, California Academy of Sciences, San Francisco, CA (Accession Numbers 611045–611047).

1959: Emile Manguin—In 1960 Manguin described and photographed 51 new diatom taxa from Karluk Lake. His diatom collection was housed at the Laboratoire de Cryptogamie, Muséum National d'Histoire Naturelle, Paris, France, but in recent years other diatomists failed to find the Karluk material at the museum (Kociolek & de Reviers 1996). These Karluk diatoms were originally collected by Douglas K. Hilliard of the Arctic Health Research Center, US Public Health Service, Anchorage, AK, and sent to Manguin (1960) for his research.

Bryophytes

1901–1902: William Titus Horne (1876–1944)—At least eight bryophyte specimens from the Karluk area are present at the New York Botanical Garden, Bronx, NY.

1954: Jones D. Reeves—While working as a FWS summer field assistant, Reeves collected bryophytes from the Karluk Lake area for the Museum of Oklahoma A & M, Tahlequah, OK.

Vascular Plants

1889: Tarleton Hoffman Bean (1846–1916)—85 plant specimens that Bean collected from the Karluk area in August 1889 are present in the US National Museum, Washington, DC, while 126 specimens are located in the Field Museum of Natural History, Chicago, IL.

1897: Trevor Charles Digby Kincaid (1872–1970)—Plants that he collected from the Karluk area in July 1897 are present in the US National Museum, Washington, DC; University of Washington Herbarium, Seattle, WA; and University of Michigan Herbarium, Ann Arbor, MI.

1897: Walter Harrison Evans (1863–1941)—Evans worked as a botanist for the US Department of Agriculture, Office of Experimental Stations. Plants he collected from the Karluk area in July 1897 are present in the US National Museum, Washington, DC.

1901–1902: William Titus Horne (1876–1944)—A large collection of plants from the Karluk area is present at the New York Botanical Garden, Bronx, NY. Horne worked at the Karluk River hatchery in 1901–1902. He collected the type specimen of the birch *Betula hornei* at Karluk in August 1902; the type can be viewed at the New York Botanical Garden website. (Available at: http://sweetgum.nybg.org/vh/specimen.php?irn=398554; accessed 29 July 2011). On 8 December 1903, Horne presented a paper entitled "The Vegetation of Kadiak Island, Alaska" to The Torrey Botanical Club in New York, based on his Karluk plant collections, which included aquatic macrophytes and algae from the river, small tributary streams, ponds, and bogs. A summary of his talk was published in the club's scientific journal in 1904 (Earle 1904), with about 50 plant species mentioned from four plant communities (low-lying *Vaucheria* bogs, grasslands, high-lying peat bogs, and alpine).

1903: Cloudsley L. Rutter (1867–1903)—230 plant specimens collected from the Karluk area in May–August are in the US National Museum, Washington, DC (Hulten 1940). Rutter's plant specimens from Alaska are also present in the Arnold Museum and Harvard University Herbarium, Harvard University, Cambridge, MA; and University of Copenhagen Botanical Museum, Denmark (Vegter 1983).

1904: Charles Vancouver Piper (1867–1926)—Plants that Piper collected from the Karluk area in July 1904 are present in the US National Museum, Washington, DC. Apparently, some of these specimens are also present at the University of Copenhagen Botanical Museum, Denmark, and Rijksherbarium, Leiden, Netherlands. Piper, an Agrostologist for the US Department of Agriculture, visited Alaska for two months in the summer of 1904 to collect plants and to determine which grasses and forage plants were most important for the region's grazing lands. He prepared a report on the most common grasses and forage plants on Kodiak Island and described early attempts by residents to raise cattle, sheep, and goats (Piper 1905).

1926: Willis H. Rich (1885–1972)—It is likely that Rich's collection of aquatic plants from Karluk Lake was originally deposited in the Dudley Herbarium of Stanford University, but in 1976 was transferred to the California Academy of Sciences, San Francisco, CA. A list of plants collected by Rich at Karluk Lake is located at Branner Library, Stanford University (G4372.K28 1926.R5).

1950: US FWS—A small collection of 15 pressed plants from Karluk is located in the National Archives and Records Administration, Anchorage, AK (Record Group 22). These plants are mainly aquatic macrophytes, sedges, and rushes.

1954: Jones D. Reeves—Reeves made a plant press while working as a FWS summer field assistant and collected specimens from the Karluk Lake area for the Museum of Oklahoma A & M, Tahlequah, OK.

1962: Eric Hulten—Hulten collected plants near Pinguicula Lake (Barnaby Lake) and the lower Karluk River in June. Specimens are located at the Botanical Museum, University of Lund, Sweden, and at the Swedish Museum of Natural History, Stockholm, Sweden.

1964–65: Richard Blott—Blott made a large collection of vascular plants at Karluk Lake while working as a FWS Seasonal Biologist, but the location of his collection is unknown.

1994: Carolyn L. Parker—Many plants collected at Camp Island and north of Karluk Lake are located at the University of Alaska, Museum of the North, Fairbanks, AK.

Invertebrates

1889: Tarleton Hoffman Bean (1846–1916)—Marine invertebrates (copepods and isopods) collected at Karluk by Bean are located in the US National Museum of Natural History (NMNH# 38570–38573, 39342, 67672). The collected copepods are the salmon sea lice, *Lepeophtheirus salmonis*.

1896: Cloudsley L. Rutter and Arthur W. Greeley—In late 1896, Rutter and Greeley collected bird lice (order Phthiraptera) from willow ptarmigan, dippers, and chickadees at Karluk. These specimens are located in the Essig Museum of Entomology, University of California, Berkeley.

1903: Cloudsley L. Rutter (1867–1903)—Marine invertebrates collected at Karluk by Rutter are located in the US National Museum of Natural History. Apparently, the stomach contents of juvenile sockeye, coho, and Chinook salmon that Rutter collected in June and July 1903 at Karluk Spit and Lagoon were later examined by Bradley (1908) for the amphipod *Corophium salmonis* at the University of California, Berkeley, and likely were retained in this collection.

1926–30: Willis H. Rich (1885–1972)—Rich collected zooplankton from Karluk, Thumb, and O'Malley Lakes and originally sent these samples to Chauncey Juday at the University of Wisconsin, where they may be deposited in the zoological museum.

1939–41: William M. Morton (1905–1981)—Freshwater mollusks taken from charr stomachs at Karluk Lake were sent to taxonomic specialists at the US National Museum of Natural History for identification in 1950 and these specimens were likely added to this collection. Likewise, freshwater leeches found in charr stomachs at Karluk and Thumb lakes were also sent to the same museum and added to its collection—*Glossiphonia complanata* (NMNH# 37321) and *Erpobdella punctata* (NMNH# 37111).

1955–56: Philip R. Nelson and Gary Lyle Seawright—Zooplankton collected by both FWS biologists from a small pond north of Spring Creek, Karluk Lake, are located at the US National Museum of Natural History (NMNH# 141767, 285273). These plankton samples were originally collected for scientists at the Arctic Health Research Center, Anchorage, AK.

1956: Douglas K. Hilliard—Hilliard worked for the Arctic Health Research Center, US Public Health

Service, Anchorage, AK, and collected zooplankton at Karluk Lake. A few of his specimens are present at the US National Museum of Natural History (*Diaptomus pribilofensis*—NMNH# 210770).

1958: US FWS—Copepod gill parasites (*Ergasilus auritus*) collected from Karluk River fish are located in the US National Museum of Natural History (NMNH# 107547)

Birds

1889: Tarleton Hoffman Bean (1846–1916)**—**Bean collected birds from the Karluk area for the US National Museum, Washington, DC.

1896–97, 1903: Cloudsley L. Rutter (1867–1903)—The bird specimens that Rutter collected from Karluk were initially deposited in the Stanford University zoological museum, but later these were transferred to the California Academy of Sciences, San Francisco, CA. Specimens included at least 15 species—common raven, bald eagle (skin and eggs), rock sandpiper, rock and willow ptarmigan, American dipper, black-capped chickadee, black-billed magpie, northern shrike, savannah sparrow, fox sparrow, song sparrow, white-crowned sparrow, pine grosbeak, and snow bunting. Another four bird skins from black-billed magpie, common redpoll, and rosy finch were collected by Rutter at Karluk in 1896–1897 and eventually deposited in the Museum of Vertebrate Zoology, University of California, Berkeley. During this same period, Richard C. McGregor obtained bird skins of pine grosbeak from Karluk (probably originally collected by Rutter), these now being located in the Museum of Vertebrate Zoology. On 17 May 1903 Rutter found a tundra swan's nest (*Cygnus columbianus*) at Karluk Lake and collected six eggs for Barton Warren Evermann. One egg was broken, but five of these swan eggs were eventually included in the Richard Magoon Barnes egg collection and are presently held in the Illinois State Museum, Springfield, IL.

Two immature bald eagles in a cottonwood tree nest, Karluk Lake, 1960. (U.S. Fish and Wildlife Service, National Digital Library, FWS-6515)

1897: Arthur W. Greeley—Two bird species (rosy finch and northern fulmar) collected by Greeley at Karluk are located at the California Academy of Sciences, San Francisco, CA

1926–29: Willis H. Rich and Seymour P. Smith—The field notes of both biologists document that many bird eggs were collected in the Karluk Lake area for Dr. Harold Heath, Stanford University, but the present location of this large egg collection is unknown. Originally, they may have been deposited in the Stanford University museum, but presently can not be located in the California Academy of Sciences, San Francisco, CA. At least one golden-crowned sparrow egg collected by Smith at Karluk eventually was deposited in the Museum of Vertebrate Zoology, University of California, Berkeley, CA

1954, 1956: John Q. Hines—Hines collected birds from the Karluk area for the natural history museum in the Wildlife Department, Humboldt State University, Arcata, CA. At least 13 species were obtained in the Karluk area, though present museum records indicate that some specimens are missing. Hines worked as a FWS stream guard at Karluk in 1954 and 1956.

Fishes

Prehistoric: Alutiiq Museum, Kodiak—This museum archives fish body parts (scales, vertebrae, and other bones) recovered in archaeological excavations at and near Karluk. The material includes salmon and various marine species (cod, halibut, and others).

1889: Tarleton Hoffman Bean (1846–1916)—Bean collected fishes from the Karluk area for the U.S. National Museum, Washington, DC.

1896–97, 1903: Cloudsley L. Rutter (1867–1903)—Rutter collected fishes from both freshwater and marine habitats at Karluk and placed specimens in the Stanford University Museum (these fishes are now at the California Academy of Sciences) and U.S. National Museum. He published a report on tide-pool fishes at Karluk (Rutter, 1899). Rutter may have collected fishes from the Karluk area in 1894 while aboard the

Grampus, these specimens being deposited in the US National Museum.

1925: Charles H. Gilbert (1859–1928)—Specimens of Karluk's sockeye salmon (SU 25226) are located at the California Academy of Sciences, San Francisco, CA

1926: Willis H. Rich and Seymour P. Smith—Specimens of Karluk's sockeye salmon are located at the California Academy of Sciences, San Francisco, CA

1926: Harlan B. Holmes—A shad, *Alosa sapidissima*, collected at Karluk in 1926 was deposited (SU 13629) in the Stanford University collection and was later transferred to the California Academy of Sciences, San Francisco, CA.

1933–35: Thomas Barnaby (1903–1998)—Sockeye salmon (UW 003712) and coastrange sculpin (UW 003760) that Barnaby collected from the Karluk River are located in the University of Washington fish collection, Seattle, WA.

1937–38: Allan C. DeLacy (1912–1989)—DeLacy collected a shad at Uyak Bay in 1937, Dolly Varden (UW 013792) from the Karluk River weir in 1938, and Arctic charr (UW 020737) in Karluk Lake in 1940. He also collected (with Morton) Dolly Varden (UW 020752–020755) and threespine sticklebacks (UW 025934) from the Karluk Lake basin in 1939–1941. These are in the University of Washington fish collection, Seattle, WA.

1939–40: William M. Morton (1905–1981)—Morton collected Arctic charr (UW 004776, 020745, 041176–041177, 041182–041183), Dolly Varden (UW 004777, 020756, 028781, 028786, 028788, 041156–041188), juvenile salmon (UW 041158–041160, 041171–041172, 041186, 041190), threespine stickleback (UW 004998, 041189), and coastrange sculpin (UW 005035, 041175) from the Karluk Lake and River basin in 1939–1941, these being located in the University of Washington fish collection, Seattle, WA. He also collected (with DeLacy) sockeye salmon (CAS 13153), Chinook salmon (CAS 13177), Dolly Varden (CAS 60559), and Arctic charr (CAS 60575), these being located at the California Academy of Sciences, San Francisco, CA.

1956: Douglas K. Hilliard—He collected sockeye salmon at Karluk Lake, these being located at the University of Alaska, Museum of the North, Fairbanks, AK.

1959: U.S. Fish and Wildlife Service—Arctic charr collected from Karluk are located in the University of Washington fish collection, Seattle, WA.

1961: Benson Drucker (1931–2000)—Coastrange sculpins that Drucker collected at Karluk Lake are located at the University of Alaska, Museum of the North, Fairbanks, AK.

1889–1998: U.S. National Museum of Natural History—This fish collection contains Karluk specimens of all eleven fish species known to occur in the lake and river—coastrange sculpin, threespine stickleback, ninespine stickleback, Chinook salmon, chum salmon, coho salmon, pink salmon, sockeye salmon, steelhead, Arctic charr, and Dolly Varden. Collections were made by many biologists.

Mammals

1896–97: Cloudsley L. Rutter (1867–1903)—Mammals that Rutter collected in the Karluk area were added to the Stanford University Museum and later these were transferred to the California Academy of Sciences, San Francisco, CA. Specimens included river otter (*Lontra*), vole (*Microtus*), ermine (*Mustela*), and fox (*Vulpes*).

1927: Seymour P. Smith—While doing his fisheries work at Karluk Lake in 1927, Smith shot a very large brown bear, which is now displayed at the U.S. National Museum, Washington, D.C. (Dodge, 2004).

1930: Claude H. Barr—At least two adult brown bears (male and female) were shot at Karluk Lake (Barr, 1931) and fully mounted by Julius Friesser for display in the Mammal Hall, Illinois State Museum, Springfield, IL. Possibly two other younger bears were also obtained. The bears were displayed in a diorama of the Karluk Lake region for a number of years (Eifert, 1941), but eventually this scene was dismantled and at least three of the four Karluk bears were placed in storage at the museum. According to the curator, the male bear is still in the museum collection, but not the female bear. In 2006 a photograph of the mounted Karluk male bear was present at the Illinois State Museum website.

1952: Roy R. Lindsley—On 23 May 1952 at Karluk Lake, FWS biologist Lindsley killed the largest Alaskan brown bear ever recorded (based on skull size). The male bear (about 540 kg) was taken to complete a planned Alaskan exhibit at the Los Angeles County Natural History Museum (Lindsley, 1978). The fully mounted bear remained on display at the museum until about 1987, when it was donated to Tunghai University Natural History Museum in Taichung, Taiwan (Dodge, 2004).[1] The Los Angeles County Nat-

[1] Jim Dines, Mammalogy Collections Manager, Natural History Museum of Los Angeles County, Los Angeles, CA, personal commun. with Richard L. Bottorff, 2006.

ural History Museum retained the record bear skull in their collection and presently has a permanent diorama that exhibits two other Karluk Lake brown bears, a sow and a cub, taken by Fred Henton in 1938. The part of this diorama that shows the sow can be viewed on the museum's website. (Available at: http://www.nhm.org/site/explore-exhibits/permanent-exhibits/north-american-mammals/grizzly-bear; accessed 29 July 2011). The museum also has a partial skeleton of a Karluk brown bear taken near Cascade Creek in May 1976.

1954: Jones D. Reeves—Mammals, especially lemmings, were collected by Reeves from the Karluk Lake area for the Museum of Oklahoma A & M., Tahlequah, OK.

1958: Robert C. Feuer—Feuer collected the skins and skulls of voles, short-tailed weasels, river otter, and bats from the Karluk Lake area while working as a FWS Seasonal Biologist. Most specimens were deposited at Tulane University, New Orleans, LA. The *Microtus* specimens were divided between Tulane University, University of Florida, and University of Michigan. He published a short paper on these mammals (Feuer, 1958).

1960s: Numerous Collectors—Many brown bear skulls were collected from different sites around Karluk Lake and archived at the University of Alaska, Museum of the North, Fairbanks, AK.

1963–1965: Jerry R. Loll—He collected the skins and skulls of tundra voles and a red fox from the Karluk Lake area while working as a FWS Seasonal Biologist. Some specimens may be in the mammal collection at Florida State University, Tallahassee, FL, while others are in the personal collection of Jerry R. Loll, Indialantic, FL.

About the Authors

Richard Gard

Richard Gard's interest in fishes began when he spent eight years as a Research Zoologist at the University of California Berkeley's field station at Sagehen Creek. He then moved to the Auke Bay Laboratory in Juneau, Alaska where he headed the sockeye salmon research program at Karluk Lake. After a few years on the fisheries faculty at Colorado State University, he moved back to Alaska to start a fisheries program at the University of Alaska, Juneau, and is now an Emeritus Professor of Fisheries. He has authored numerous papers on fishes and gray whales. Dr. Gard has BA, MA, and PhD degrees in Zoology from the University of California, Berkeley.

Richard Lee Bottorff

Richard Lee Bottorff has been fascinated with the biology of rivers and lakes since childhood and has worked as an aquatic biologist in Alaska, California, and Colorado for over 40 years. His biological research has included studies of springs, rivers, lakes, and watersheds, including their hydrology, fishes, and aquatic invertebrates and plants. Richard has an MS in Fisheries from the University of Alaska and a PhD in Aquatic Ecology from the University of California, Davis. (Photo by Loren D. Bottorff, 2012)